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The development of the ascus and the occurrence of giant ascospores in Coccomyces hiemalis[1]

MYRON P. BACKUS

(WITH TWO TEXT FIGURES AND PLATES 29–32)

This communication is devoted to a study of the development of the ascus in *Coccomyces hiemalis* Higgins on a single host, *Prunus cerasus*. Morphological, cytological, and experimental studies on other phases of development are already well advanced, and it is hoped that these may lead to a full understanding of the life cycle of this species.

Coccomyces hiemalis was first described by B. B. Higgins in 1913. He found the ascocarps of this fungus on the overwintered leaves of *Prunus avium* and by inoculation experiments showed this to be the perfect stage of a *Cylindrosporium* which had often been referred to *C. padi* Karst., and which had long been recognized as the causal organism of the destructive "leaf-spot" disease of sweet cherry. The following year (1914) Higgins was able to demonstrate that this same species is also responsible for "leaf-spot" of *Prunus cerasus* and *P. pennsylvanica*. Keitt (1918) showed that it might in addition attack *Prunus mahaleb*. In his second paper (1914) Higgins outlined the chief morphological features in the development of the fungus, but he made no attempt to study it cytologically.

The order Phacidiales, to which *Coccomyces hiemalis* belongs, is of special interest as a transition group, and but few species in it have yet been subjected to thorough investigation. In only one species has a cytological study of the ascus been made (Jones, 1925). *Coccomyces hiemalis* shows a close resemblance in many features to some of the lichens, a group that has figured prominently in all discussions of the phylogeny of the Ascomycetes, and the study of which, despite several excellent papers dealing with them, may be said to be just getting under way. The presence of prominent trichogynes developing in interesting relation to the numerous microconidia in the cherry leaf-spot fungus especially demands that the phases of development in this organism relating to the initiation of the ascocarp, be subjected to the most careful scrutiny, particularly in view of the apparent homology of these microconidia with the spermatia of the rusts, which have now been shown to be functional elements. Re-

[1] The work here reported was begun while the writer was a graduate student at the University of Wisconsin but was executed largely at the New York Botanical Garden during the tenure of a National Research Fellowship in the Biological Sciences.

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cent demonstrations in the case of certain heterothallic Ascomycetes that the microconidia may function in the capacity of fertilizing agents. (Drayton, 1932; Dodge, 1932; Ames, 1932), are of the greatest interest and significance, and fall into line with the basic idea held by Stahl (1877) and some of the older authors, that the spermatia of the lichen fungi with which they worked, function as fertilizing elements by attaching themselves to trichogynes. In the more recent work, unfortunately, almost no cytological data are yet available.

We do not know whether the cherry leaf-spot fungus is heterothallic or homothallic. However, an experiment which it is hoped may settle this point is under way. It may be of interest here to indicate briefly the methods employed in a preliminary experiment. This first trial has involved the isolation of the eight spores from a single ascus. Since, insofar as we know, ascocarps cannot be produced on artificial media, it was necessary to resort to use of the natural substratum. Large numbers of conidia of each ascospore strain were grown on agar and at the proper time cherry trees were inoculated. The various ascospore strains were used alone and in combination, and the inoculated trees were subsequently kept in isolation. The leaves infected with the fungus were collected at leaf-fall and left out-of-doors in isolation cages over winter. The results of this preliminary trial, which will be detailed elsewhere, have afforded some very interesting clues and have given us some valuable data. They do not settle with certainty, however, the question of heterothallism in this species. Many difficulties beset such an experiment, and many complicating factors are involved. Another experiment based on the information gained from the preliminary test is being conducted on a larger scale and under improved conditions; there is every reason to believe that the question of heterothallism in *Coccomyces hiemalis* can thus be definitely settled.

MATERIALS AND METHODS

The material for the present investigation of the development of the ascus—overwintered leaves of the sour cherry, bearing ascocarps of the "leaf-spot" fungus in various stages—was derived from a variety of sources. Approximately half was collected by the writer during the springs of 1929–'31 at Madison, Wisconsin, in the orchard of the University of Wisconsin and in private orchards in the vicinity. In the fall of 1931, through the co-operation of various plant pathologists and county agents,[2] I was able to assemble at the New York Botanical Garden infected leaves, collected at the time of leaf-fall, from Penn., N. J., and northwestern N. Y.

[2] I am indebted in this connection to W. O. Gloyer, W. H. Martin, J. F. Adams, H. H. Whetzel, E. M. Hildebrand, and especially to J. G. Goodrich.

state. These were overwintered at the Botanical Garden and drawn upon as a source of supply for fixations throughout the spring of 1932. I also received from Sturgeon Bay, Wisconsin, and Lockport, N. Y. during April and May 1932, freshly collected leaves that had overwintered in the orchards.[3] For still another source of material I am indebted to Prof. G. W. Keitt of the University of Wisconsin who very kindly turned over to me a quantity of imbedded material from his files, representing fixations made by him from orchards near Madison, Wisconsin during the springs of 1915–1917.

In some instances fixation was made immediately after the leaves bearing the fungus were brought into the laboratory and had been washed off, and even occasionally in the field at the time of collection. But for the most part they were allowed to remain in a moist chamber between damp filter papers for varying lengths of time before fixations were made. This was an essential procedure in most cases. The development of the asci of this fungus extends over a considerable period (several weeks, in many cases) and the ascocarps dry out repeatedly during this time. Material brought into the laboratory in a dry state must be placed under conditions favorable for the "recuperation" of the fungus before fixation for cytological study. Fixations were made at from three to seventy-two hours after the leaves were placed in the damp chamber, and two series were made with fixations at two-hour intervals over a 24-hour period.

Flemming's weaker and medium solutions, dilutions of these with equal parts of distilled water, a modification of Flemming's weak with ten times the normal amount of acetic acid recommended to me for fungi by Dr. C. W. Emmons, Carnoy's B, Carnoy's B followed by Flemming's weak, formol-acetic-alcohol, Bouin's, Allen's Modification of Bouin's, Navashin's and Gilson's were among the fixatives tried. Regular Flemming's weak and Flemming's weak diluted one half were found to be about the best of the Flemming mixtures, and were a great deal used. Emmons' modification, tried only in the last fixation series, however, gave results nearly on a par with those obtained with these two other solutions. Allen's modification of Bouin's formol-acetic-alcohol, and Carnoy's B were also employed quite extensively and for certain things were found superior to Flemming's. Sections were cut from four to ten microns thick, the most at six and seven microns. Flemming's triple stain was tried, but Heidenhain's iron-alum haematoxylin, especially with counter-stains of erythrosin or fast green, was found so much superior in general that it was almost exclusively used.

[3] E. C. Blodgett and J. G. Goodrich provided me with this material and I am greatly obliged to them for their courtesies.

In addition to the cytological preparations made in the fashion described above, slides of another sort were made for supplementary study. Fresh ascocarpic material was dissected, teased out, and crushed in aceto-carmine. These mounts proved to be very helpful.

NORMAL ASCUS DEVELOPMENT

The time at which asci first begin to form in the spring has been found to vary with the weather conditions. Under the conditions of temperature, etc. which usually prevail in Wisconsin in the vicinity of Madison the first appearance of asci may be expected in the early part of April. It was found, however, that in material overwintered in New York City during the winter of 1931–'32, which was unusually mild and practically snowless, they began to form as early as the middle of March. By bringing leaves inside and leaving them in a moist chamber for a few days asci can sometimes be induced to appear several weeks prior to the time of their formation outside. As has already been pointed out, the development proceeds quite slowly, and it was not until after the middle of May that mature spores were found in abundance under either Wisconsin or New York conditions. Asci in various stages are to be found in a single fruiting body.

In mounts prepared by crushing out young ascocarps in aceto-carmine, it was found quite simple to demonstrate that the asci in *Coccomyces hiemalis* arise by the well-known process of crozier formation. Figures 52–54 show photomicrographs of croziers as seen in such preparations. In good mounts even nuclei can be distinguished. Text-figure 1 shows sketches of typical croziers as observed in these aceto-carmine slides. The tip of the ascogenous hypha bends over (text-fig. 1, A), walls are formed in the familiar fashion, and there can now be observed (pl. 29, fig. 1) a tip cell with its single nucleus and the penultimate cell with two nuclei which proceed almost immediately to fuse (pl. 29, figs. 3–5; also text-fig. 1). In a considerable number of instances the tip cell was seen to have fused back with the antepenultimate cell (text-fig. 1, I, J, K, L, etc.; also pl. 29, fig. 5). But such a cell fusion is apparently not an essential feature for it not infrequently fails to occur (text-fig. 1, N, O, R, etc.). As the penultimate cell grows out to become the young ascus, the fusion nucleus increases in size and moves upward in the elongating sac (text-fig. 1, N, P, and R; also pl. 29, fig. 6). Text figure 1, E and M show interesting situations which might be interpreted as lending support to the theory of Moreau and Moreau (1922; 1928) to the effect that clamp connections occur along ascogenous hyphae. Cases occasionally seen in aceto-carmine slides where the crook cell of a crozier was apparently proliferating to form a short ascogenous branch instead of swelling up to form an ascus

in the usual manner, give us a suggestion of how the situations pictured in the figures just mentioned, may have come about.

Variations in form of the ascus in the leaf-spot fungus are interesting. Some of the asci have very long bases. This is correlated with the fact that in some instances they may arise relatively deep in the stroma. This point will be further discussed in another paper in which the development of the ascogenous system will be specially considered. Despite the general slowness of the asci in maturing, there is evidence that the early stages of growth proceed with comparative rapidity under normal conditions. The young spore sac is usually rather slender and quite evenly filled with dense cytoplasm. The nucleus frequently fills practically the entire cross-

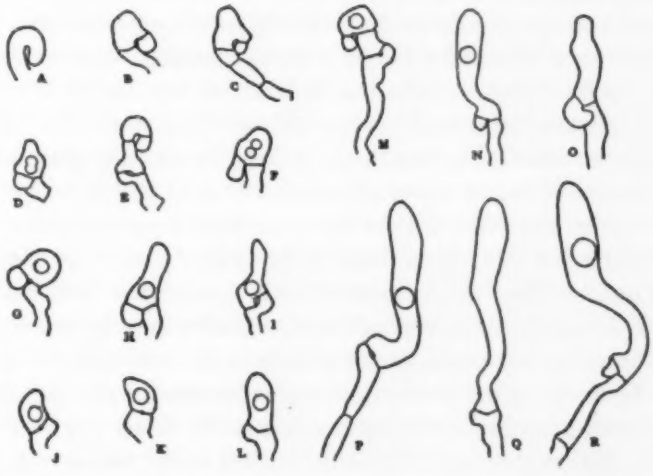

Fig. 1. Croziers and young asci of *C. hiemalis* (from aceto-carmine preparations). Various magnifications.

section of the sac at this stage and may sometimes even be slightly elongated, due apparently to lack of room for it to assume a more spherical contour. Considerable variation exists, however. Plate 29, figure 6, shows an ascus about one-third grown. It shows particularly well the details of nuclear structure to be considered below. It is fairly typical in its general form. As growth proceeds, the ascus continues to swell in its upper portions and takes on the typical clavate form. Once the size shown in plate 29, figures 7 and 8, is attained, there is little further increase until after the spores are formed.

During the growth of the ascus the cytoplasm tends to become aggregated toward the top of the sac especially as the ascus ages. The lowermost regions become practically devoid of stainable contents, while the upper

third of the ascus is seen to be filled with dense, finely granular cytoplasm, the sporeplasm, which in some cases grades off quite imperceptibly into the watery vacuolate epiplasm below, but which usually is quite sharply delimited, especially as the ascus increases in age. Moreover it is rather characteristic for preparations to show invagination of this conspicuous densely-staining mass by the thin plasma below it, a situation sometimes seen in extreme expression as shown in plate 29, figure 13. The dense sporeplasm in the upper part of the ascus is destined to be the seat of activity for the phenomena leading to spore formation.

The large fusion nucleus lies in the dense cytoplasm, often slightly below the center of the mass, and it frequently takes up its position to one side of the ascus (pl. 29, fig. 7). It attains a considerable size—sometimes measuring as much as 7.5μ in diameter. When compared with the definitive nucleus in a form like *Verpa bohemica*, which Komarnitzky (1914) reports has a diameter of up to 16μ, it is not so big, but it is nevertheless a very conspicuous body and is especially striking since the cytoplasm in which it lies is remarkably free from the heavily staining granular material which is so abundant in many Ascomycetes and which I have observed to be very prominent in another Phacidiaceous form, *Diplocarpon Rosae*. Occasionally a few densely stained bodies may be seen, particularly in a zone just outside the nuclear membrane in *Coccomyces hiemalis*, but they are scarce. Exceptionally, several large vacuoles may be present (pl. 29, fig. 7). Numerous big vacuoles are visible in the sporeplasm of the ascus shown in figure 48, which is of interest also because of the fact that in this particular well-grown primary ascus nucleus two relatively small nucleoles are visible. Either the nucleoles of the fusing nuclei failed to unite in this case or perhaps the situation has resulted from fragmentation of a single large nucleole previously present. In any case the example is unique, no others like it having been observed.

The definitive nucleus shows typically a large nucleole, and the chromatin is conspicuous. By far the greatest number of asci observed in the uninucleate condition showed the nuclear network more or less like that shown in plate 29, figs. 7 and 8. This was found to be the case in all of the material, regardless of the fixative used. Since it is already observable (though usually not so clearly defined) in only half-grown asci (fig. 6) and in such predominance among all the asci containing a single nucleus, it is evident that it must represent a considerably protracted stage. The interpretation of the nuclear organization here is not by any means easy. The essential features of it, insofar as I have been able to observe and interpret them, will now be considered.

There is present a framework of clearly distinguishable linin in the

form of a thin thread or threads winding throughout the nuclear cavity, the various portions of which occasionally give the impression of anastomosing with each other; but again in other instances extensive segments appear clearly to lie free in loops (fig. 8, a); very conspicuous beads of chromatin are imbedded in the linin at intervals, (figs. 7 and 8). Just how to interpret the "beads" is not clear. Whether they represent distinct chromatin masses, perhaps of the nature of prochromosomes, or are to be regarded as less definite, possibly chance aggregations in the thread or concentrations at focal points in the framework, of chromatin material in a disperse phase, I am not prepared to say. There is considerable resemblance between the nuclei in *Coccomyces hiemalis* and the figures given us by Bagchee (1925) for *Pustularia bolarioides* where likewise numerous chromatin units figure prominently in the nuclear organization. In this form Bagchee reports the chromatin beads to be very distinct chromatin entities of definite number, perfectly related to the number of chromosomes. She describes the formation of bivalent chromosomes in the prophases of the first division by the bringing together of the beads which she designates as "half-univalents," first in pairs and then finally, at the beginning of second contraction, in tetrads. To what extent the chromatin bodies in the nuclei of the cherry leaf-spot fungus are comparable to those in Bagchee's *Pustularia*, I am unable to state. It has not been possible to assign any definite number to these bodies in the species of *Coccomyces* studied. Moreover their size seems to vary, and I could not follow any of the complicated phenomena reported for *Pustularia* as effecting the association of the beads. Nuclei showing clearly defined spiremes also are to be found occasionally (fig. 9). Frequently the spiremes stain quite evenly throughout, but it must be admitted that they sometimes also show suggestions of beads. I have seen suggestions of double threads here, as well as earlier. It seems probable that the stage where chromatin beads are so much in evidence is to be interpreted as a protracted early prophase and that the distinct spiremes represent a later prophase development. It is conceivable that the chromatin bodies might maintain their individuality through this latter stage, although in most cases little trace of them can be found. *Coccomyces* is by no means the most favorable of material for study of these early prophases. With the exception of two cases where possible contraction phenomena were indicated, I have been unable to identify in *Coccomyces hiemalis* the ordinary features characterizing the prophases of heterotypic division.

It will be remembered that it is characteristic in many Ascomycetes for the fusion nucleus to enter very early into prophase of a heterotypic division. In *Humaria rutilans* Fraser (1908) reported that the nuclei in

the young ascus cell go into prophase independently even before fusion. In *Peziza vesiculosa* where fusion of the nuclei was seen to be delayed until the ascus had attained considerable size, it was also reported (Fraser and Welsford, 1908) that in the material examined the two nuclei were already showing first meiotic contraction at the time they fused. In these and similar forms the fusing nuclei are of quite large size—over 5μ in diameter—and the amount of increase in the size of the fusion nucleus until its maximum is reached is not great. A similar situation obtains in *Phyllactinia corylea* (Harper, 1905). In the species of *Coccomyces* under consideration quite a different situation is found. The nuclei as relatively minute bodies fuse in the crozier without delay. The growth in volume of the definitive nucleus from the time the fusion is completed until maximum size is attained is enormous, paralleling the growth of the ascus in volume (cf. figs. 5 and 7). The small size of the very young primary ascus nucleus, in addition to the difficulties in obtaining good cytological preparations for this stage, renders it impossible to gain any accurate idea of the condition of the chromatin at this time. However, it seems quite unlikely that any such precocious entrance into prophase as Fraser found for *Humaria rutilans* occurs. On the contrary the evidence points to the probability that the fusion nucleus increases to several times its original volume before such stages emerge. These differences in relative size of nuclei at time of fusion and the differences in nuclear activity in these forms are interesting. How far they are to be correlated with mode and rate of development of the ascocarps in the species concerned, should be worth consideration.

We need not consider in great detail the three successive nuclear divisions in the ascus. The division figures here are not large and in general agree in character with figures already published for many other Ascomycetes. In all three divisions the same number of chromosomes—namely, four—seem to be present at the equatorial plate stage. No anaphase stages were seen, and in telophase the individual chromosomes could not, of course, be identified. The spindles were found to be intranuclear, and small densely-staining centrosomes were identified. The spindle of the first division lies more or less parallel to the long axis of the ascus. A division figure at equatorial plate is shown in figure 10. At telophase the chromosomes are grouped in a dense mass at the poles, and a remnant of the spindle usually can be seen lying between the two. The telophase of the first division shows the same features as that of the second, which is illustrated in figure 13, and will be described below. The two reorganized daughter nuclei grow to conspicuous bodies which, like the primary ascus nucleus, show chromatin-bead structure in favorable preparations (fig. 11).

The spindles of the second division lie usually somewhat diagonally in the ascus (fig. 12). Figure 13 shows that the spindles may lie almost parallel to the long axis of the sac. It shows, moreover, an unusually interesting relation of the position of the division figures to the contour of the dense cytoplasm, which is here extremely invaginated. Incidentally it shows also the characteristics of the telophase—the chromosomes closely grouped at the poles and the remnant of the spindle (which elongates somewhat after the nuclear membrane disappears) visible as a rather thick lightly staining thread between them, while in the cytoplasm midway between the two chromosome masses, the disorganizing nucleole of the mother nucleus may still be identified. The position of the nuclei at the four-nucleate stage is indicated in figures 14–16. Chromatin beads can be identified in some cases, but in these smaller nuclei they are usually not clearly distinguishable. Asci at the four-nucleate stage are quite abundant. This fact leads to the assumption that at this point a considerable rest period ensues (cf. observations of Brooks (1910) on *Gnomonia erythrostoma*, Bagchee (1925) on *Pustularia*, etc.). Following the third division (fig. 16) the eight small nuclei move rapidly toward the walls of the ascus and there develop prominent beaks and cut out the spores with the usual accompaniment of astral rays (figs. 18 and 19).

Not very many Ascomycetes with long ascospores have been studied cytologically, and there seems to be some confusion in the literature concerning the exact process by which these spores are developed. Maire's figures (Maire, 1905), showing the very young spores of *Rhytisma acerinum* as more or less spherical or ovoid structures which only later elongate, are doubtless correct. Faull (1912) indicates a similar situation in the development of elongated ascospores in *Laboulbenia chaetophora*, and Jolivette (1910) does likewise in the case of *Geoglossum glabrum*. Lewis' figures for *Pleurage zygospora* (Lewis, 1911) indicate that here the spores begin as very small, rather broadly ellipsoid bodies which subsequently undergo extensive elongation and finally differentiation. Jones' (1925) figures and description of spore development in *Rhytisma acerinum* are less clear. He suggests the probable functioning of vacuoles in the delimitation process; and one gets the idea from his paper that he believes that the spores as first formed tend to have an elongate shape. The crude figures of Lewton-Brain (1901) for *Cordyceps ophioglossoides*, show the spores delimited as filiform structures.

In my study I have been able to show clearly that in *Coccomyces hiemalis* the spores are cut out as very nearly spherical bodies which only through a process of elongation and growth finally assume the shape typical of the mature spores of this species (see text-fig. 2). In figure 20 the

delimitation process has just been completed. In figures 21 and 22 the spores are older and they stand out in sharper outline. Perhaps there has already been some thickening of the spore membranes. The young spores lie closely packed in the upper part of the ascus, the position previously occupied by the sporeplasm from which they were cut out. The epiplasm is at first dense but thins out as the spores develop. Figure 55 shows an ascus at the stage in question, from an aceto-carmine *in toto* preparation. The normal position of the spores seems to have been upset during the crushing of the ascocarp. But the globular form of the spores in focus is evident.

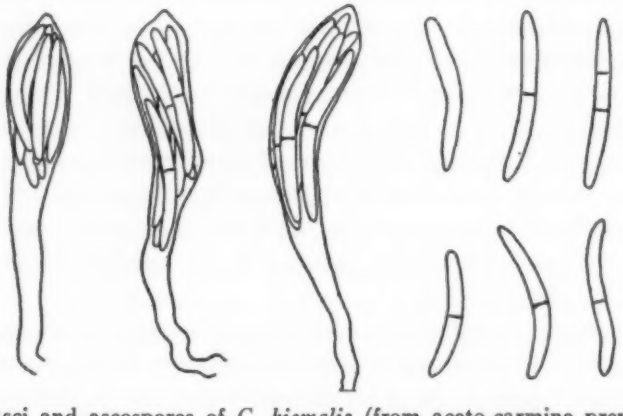

Fig. 2. Asci and ascospores of *C. hiemalis* (from aceto-carmine preparations). × about 500.

The spores do not long maintain their spherical shape. They very soon start to elongate, increasing slowly in volume. Figures 23 and 24 show two successive sections of an ascus which, although in some respects abnormal, shows clearly the first stages of elongation. This ascus is larger than the average, and the spores are somewhat bigger than usual at this stage. Moreover their usually crowded arrangement is here lacking. Their shape, however, is quite typical. The ascus shown in figure 47 is also abnormal. Here only one of the eight nuclei in the sac appears to have cut out a spore. Remains of several nuclei lying free in the cytoplasm may be seen. Reference will again be made to this ascus in another connection. Figures 25 and 26 show typical asci with the elongation process considerably farther under way. The arrangement of the ascospores is characteristic, remain closely packed together and lie diagonally in the sac, parallel to one another. Often at this stage the exact limits of the individual spores are not easy to see. As the spores attain a considerable length, they slip more and more into a position parallel to the long axis of the sac. The

early elongation apparently takes place with considerable rapidity and although the spores increase in volume, this increase is not often in proportion to the change in length, with the result that the young spores at the stage following that just described, are sometimes quite thin structures (fig. 27). The final stages of elongation take place more slowly; and the spores now increase markedly in diameter while completing their growth in length (figs. 28–31).

Some general idea of the changes in size and shape of the spore nucleus during the development of the ascospores may be had from an examination of figures 20–31. The increase in size from the time the spore is cut out is considerable. As the spore assumes an elongated form, the nucleus also becomes more or less stretched out. In the thinnest young spores the contour of the nucleus may be greatly modified in conformity to the small diameter of the cell in which it lies. The nucleole usually is found near one end of the nucleus, and sometimes that is all that can be clearly distinguished, the stainability of the chromatin varying decidedly, even occasionally in spores of the same ascus (fig. 30). With the increase in diameter of the spore, the nucleus returns more or less to its normal spherical shape (fig. 31).

As the growth of the spore proceeds, the ascus increases in size. The denser materials of the epiplasm are used up more or less completely, and the ascospores usually come to fill the sac in its entire diameter. The fascicled arrangement is typical, and is represented in cross-section in figure 32. I was unable to find nuclear division in spores in any of my material. The evidence is that the original nucleus does usually divide, however; and the spore becomes septated, each segment thus formed including presumably one of the daughter, or grand-daughter, nuclei (figs. 33 and 34). Septation occurs as one of the final steps in the maturation of the spores and is accomplished only a short time before they are shot out. Most often mature spores have a single septum, less commonly two, and quite rarely three. Occasionally non-septate spores may be found (text-fig. 1). There does not appear to be perfect correlation between spore size and degree of septation.

Having thus presented a fairly detailed picture of normal ascus development in *Coccomyces hiemalis*, I shall now consider certain abnormal features.

GIANT ASCOSPORES

While studying some mounts of ascocarps dissected and crushed out in aceto-carmine, my attention was occasionally drawn to certain asci which presented an abnormal appearance. While some of the spores in these were perfectly normal, others were seen to be of unusual size and in

some instances of peculiar shape (fig. 57). Closer examination showed, further, that in every instance these asci contained fewer than eight spores. Figure 59 shows the contents of an abnormal six-spored ascus. Two of the spores are markedly longer than the four which are of normal size. The giant spores here differ only in their increased dimensions, whereas one of the two giants in the ascus pictured in figure 57, shows also very abnormal contour. Figure 58 shows what came out of an abnormal five-spored ascus in which the spores were just in process of elongation when crushed. The three central ones are larger than the outer two. Undoubtedly the central three would have elongated and grown to be giants while the other two would have developed into normal spores.

Accounts of the occurrence of giant ascospores are still something of a rarity in the literature. This is perhaps the first time that they have been reported for a parasitic species. Spores of unusual size were occasionally observed by very early mycologists but they were regarded for the most part as inconsequential. Records of irregularity in size and number of spores in an ascus are not wanting in taxonomic literature. Maire (1905), Faull (1905), and Fraser (1908) figured spores of unusual size in *Morchella esculenta*, *Neotiella albocincta*, and *Humaria rutilans* respectively. These early cytologists called attention to the abnormal character of such spores but did not discuss them further. Later workers on big spores have given them more thorough consideration and in several instances, as will be pointed out later, their studies have brought out some very interesting points and relations. Among the best known and most remarkable examples of giant spores are those found in *Neurospora*. Dodge (1927, 1928a, 1928b, 1929) reported their occurrence here in various species and hybrids and indicated their significance in relation to their genetic constitution. Recently Moreau and Moruzi (1932a, 1932b, 1932c) have described some interesting experiments they performed with big spores found in *N. sitophila*. Abnormally large ascospores are also known in *Pleurage anserina* and have been found comparable to those of *Neurospora tetrasperma*. Moreau (1914) has called attention to variability of ascospore size in *Bulgaria inquinans* and has presented an interesting study of the situation there. Very recently Zickler has produced giant spores experimentally in *Sordaria macrospora* and *Neurospora crassa* by the use of chloral hydrate and ether. In most of the instances evidence, either direct or indirect, has been brought out to the effect that more than a single nucleus is included in each giant spore at the time of its formation. Fraser (1908) figured five nuclei cooperating in the cutting out of a single giant spore in *Humaria granulata*, and Faull's (1905) drawing of the big *Neotiella* spore shows that two nuclei were included. Maire (1905) found evidence that

likewise two nuclei were involved in the formation of the big *Morchella* spore which he figured. In 1907 Dangeard published a drawing of an ascus of *Ascobolus furfuraceus* with seven spores, one of which contained two nuclei. Very recently Gwynne-Vaughan (1933) has figured a six-spored ascus of *Lachnea scutellata;* one of the six spores is an irregularly shaped giant with three nuclei. Dodge has shown clearly that a correlation exists between the number of spores found in an ascus in *Neurospora* and the presence among them of spores of unusual size, and a similar correlation is known to exist in *Pleurage anserina*, etc. "Extra-giant" spores have been found in *Neurospora* (Dodge, 1927, 1928a; Moreau et Moruzi, 1932a), and recently they have been artificially produced by Zickler (1931) especially in *Sordaria macrospora*. An extreme case where but one supergiant *Neurospora* spore is produced in an ascus, is figured by Dodge (1928a) who believes that in such a case the giant has claimed all eight nuclei present in the sac.

A paper of interest and one in which evidence is brought forth that the inequality in size among spores in an ascus may not necessarily be correlated with a difference in nuclear content at the time the spores are cut out is that of Moreau (1914), above mentioned, on *Bulgaria inquinans*, a species where irregularities in number and especially size of spores has apparently been recognized quite widely. Moreau concluded from his study that in some instances two or three nuclei are included in a single big spore, in which event the total number of spores is proportionally reduced. However, he discovered that not all the big spores were of this same cytological character. Some asci contained some big and some small spores but regardless of their size each contained only a single nucleus. The explanation for this was found to lie in the fact that there is a tendency in this species to a lack of synchrony in the nuclear divisions in the ascus. Because of this situation some spores (usually 4) are formed before the others. The assumption is that the first-formed spores are better nourished and hence grow bigger. The later-formed spores are usually perfectly viable, however. Such asci naturally contain eight spores. But in some instances the spores last cut out may be so poorly nourished that they abort, and in such a case superficial examination may show the presence of only four spores. In this species, then, the number and size of ascospores may both vary for quite different reasons.

There are to be found in the literature descriptions of other species which agree more or less closely with the form just described in showing, very frequently, asci with four large and four small spores. In two species of *Trichoglossum*, *T. velutipes* and *T. tetrasporum*, Sinden and Fitzpatrick (1930) have described a situation where only four spores in an ascus mature

and the other four degenerate after formation or remain more or less abortive. Woronin (1888) described and figured the asci of *Sclerotinia oxycocci* and *Sclerotinia baccarum*. In both of these he found, apparently with considerable constancy, four large ascospores in each spore sac and also four of much smaller size. Unlike the situation in the species of *Bulgaria* which Moreau studied, however, Woronin reported that the small spores in the Sclerotinias in question would not germinate. Unfortunately we know nothing of the cytology of the ascus either in the case of these forms described by Woronin or of the two *Trichoglossum* species above mentioned. It would be interesting to determine whether the situations here are to be explained in the same fashion as that in *Bulgaria inquinans*. There can be no doubt that nutritional relations may play a very significant part in causing variations in ascospore size. In the light of this and of our knowledge of degeneration of nuclei and spore initials under a variety of circumstances, it is apparent that without cytological study we cannot safely come to a conclusion as to the number of nuclei included in any particular spore.

I have mentioned the fact that in the cherry leaf-spot fungus, as also in some other regularly eight-spored forms, it has been ascertained that asci in which big spores occur have fewer than the normal number of spores. In several forms, as in certain species of the Erysiphaceae, *Laboulbenia*, *Meliola*, and *Keithia*, also in *Neurospora tetrasperma*, *Pleurage anserina*, etc. it is the rule. The cytological studies in which the nuclear relations in these forms are considered are of interest here because the nuclear phenomena in relation to spore formation in many of these are of the same order as those involved in the formation of giant spores. In fact, one might say that in a certain few of these forms all the spores are giants and that these are formed in definite number and regular fashion, the habit of forming them having become established as a constant character in the particular species. All except the most recent of these studies have been noted by Dodge (1928b).

Harper (1905) studied *Phyllactinia corylea* which usually shows two spores in an ascus and found that although the usual eight nuclei are formed, six degenerate and only two cut out a spore each. In the two species of *Laboulbenia* studied by Faull, *L. chaetophora* and *L. gyrinidarum*, four of the nuclei function and four degenerate, each of the four spores formed thus having a single nucleus at its initiation. Komarnitzky (1914) concluded that in *Verpa bohemica* the two spores developed each include but a single nucleus. He found that the regular triple nuclear division occurs in the ascus but reports that in his material following each of the first two divisions one of the daughter nuclei migrated out of the dense

sporeplasm into the more watery cytoplasm below, there to degenerate directly or undergo a division after which the resultant daughter nuclei would disorganize—an interesting sequence if true, but unfortunately Komarnitzky's figures are not completely convincing. We know of other forms where the reduced number of spores is due to degeneration of spore initials after they have been formed.

Podospora anserina (*Pleurage anserina*) (Wolf, 1912), which has typically four spores, was the first form in which the inclusion of more than one nucleus was reported as a phenomenon of regular occurrence. Eight nuclei are formed in the ascus and two co-operate to form each spore. Dodge (1927) found a similar situation in the four-spored species *Neurospora tetrasperma*, but he made a more complete cytological study of the ascus and gave us very interesting figures showing the actual details of spore delimitation with two nuclei co-operating. Moreover he was able to offer conclusive evidence that in that species nuclei of opposite "sex" come together in pairs, and each pair cuts out a spore capable at maturity of germinating to produce a homothallic mycelium. Dwarf spores formed as an abnormality and containing a single nucleus at origin, were found to be of one "sex" or the other. Such a spore produced a mycelium which, unless mated with the opposite strain, remained sterile. A similar state of affairs apparently exists in the four-spored form *Pleurage anserina* (Dowding, 1931), and likewise in the four-spored form of *Sordaria fimicola* (Page, 1933). Recently Graff (1932) has shown that two nuclei are included in each of the four spores of the ascus in *Meliola circinans*. In some ways the most remarkable case is that reported by Dodge (1928b) for *Keithia chamaecyparissi* where he concluded that despite the fact that only two spores are regularly formed, all eight nuclei function, four being included in each ascospore.

Our knowledge of the nuclear situation in giant spores in Ascomycetes has been arrived at not only through actual cytological observation, but also to some extent by deduction from certain cultural experiments in which the character of mycelia derived from big spores has been studied. In *Neurospora* which has played a major rôle in the giant spore studies, deductions of this kind have had an important part (Dodge, 1929, Moreau and Moruzi, 1932a; 1932b).

In the case of giant spores in *Coccomyces hiemalis* I was fortunate in obtaining some cytological data concerning the nuclear situation, which, although not complete is nevertheless interesting. In studying a relatively large number of cytological preparations of sections through ascocarps, occasionally I found an ascus with giant spores. Although thus far I have been unable to construct a complete developmental series from this scat-

tered material, yet evidence is clear that the big spores in this form claim at their formation two or more of the eight nuclei resulting from the three successive nuclear divisions. I have found to date no examples of giant spores in process of being delimited. Figure 35, however, shows an ascus where the spores have not yet begun to elongate. There are seven spores present and one of them is considerably larger than the others and contains two nuclei. In figure 36 are to be seen two more spores of interest. Comparison of their size with that of normal spores in the spherical stage at once shows these to be giants. In one of the spores—the larger of the two—there are three nuclei, while the other has two. Figure 37 shows two giant spores in early stages of elongation, each containing two nuclei. Figure 39 shows a clearly abnormal spore which, however, is apparently not yet fully grown. This giant shows an atypical shape and contains five nuclei. In figures 38 and 40 can be seen a two- and three-nucleate spore respectively. The contrast in size with normal spores is here well illustrated. The giant pictured in figure 42 shows four nuclei. But its great size would suggest that perhaps even more were present but were cut off in the sectioning. Unfortunately the rest of the ascus could not be identified in the next section. Figures 41 and 43 are of interest because of the peculiar shape of the big spores; and incidentally the spore shown in figure 43 contains six nuclei—the largest number I have observed to date. It should be pointed out that while the included nuclei may take up various positions in a big spore, as inspection of the figures will show, there seems to be a decided tendency in many cases for the nuclei to clump closely together (figs. 39, 42, 43, 45, and 46).

In certain of these asci with big spores a nucleus can be seen occasionally which has not to all appearances been included in any spore but lies free in the epiplasm, as is so common in the powdery mildews. These examples are quite rare in my material. Mention has already been made in the preceding section, of an ascus obviously not normal but without big spores where most of the nuclei seemed destined to disintegration (fig. 47). The development of all these abnormal asci may likely be perfectly normal up to a certain stage. It may well be that at some critical point adverse environmental factors of one sort or another (perhaps of small moment) obtaining at the time, disturb the delicately-balanced workings in the spore sac. This upset might conceivably be expressed in more than one way. Dodge (1928a) has given us a most interesting figure of a case in a *Neurospora* hybrid where an ascus failed to develop any spores at all but instead the wall of the ascus darkened and took on the normal markings of a mature spore. Zickler (1931) in his work seems to have obtained similar cases where whole asci took on features characteristic of mature spores.

It may not be exactly correct to speak of these in the fashion that Zickler does, as asci which have turned into single big spores. The fundamental thing here, however, seems to be that the protoplasts, although failing to function in the usual fashion, do not abort completely or disintegrate, but, with age, effect certain changes in the whole sac which normally characterize maturation phenomena in spores of the species involved. It is quite conceivable that in these cases the plasma membrane of the ascus may function exactly as the limiting membrane formed when a spore is cut out. In a certain sense, then, it may be right to speak of the transformation of one of these sacs into a single spore. But we must distinguish carefully between these types and such examples as Dodge (1928a) figures where we have a single clearly defined super-giant spore lying free in the sac, a spore very evidently delimited in the fashion characteristic of ascospores, though all the nuclei must have co-operated in the process. Zickler fails to distinguish sharply between the two types. Nothing is known of the nuclear behavior in the asci undergoing the peculiar changes just described, and none of these "asci" has ever been germinated. In any case these examples furnish us with extreme illustrations of drastic modifications of the familiar sequence of events in the spore sac, correlated doubtless with some serious upset in the mechanism. Zickler's success in producing asci with big spores in abundance by use of certain chemicals is very interesting and may open the way for an extensive and illuminating study of experimental abnormal cytology of the ascus.

In general, on the basis of the facts disclosed in the study of the cytology of the giant spores in the leaf-spot fungus, as already detailed, I believe we are safe in concluding that in *Coccomyces* the observation that there are fewer than eight spores in asci containing spores of unusual size is to be explained by the fact that the giants enclose two or more of the eight nuclei which are present as the result of the three successive nuclear divisions.

I have been unable to find any septate giant ascospores, so I cannot be sure that they ever do become septate. If they do, it would be interesting to learn the nuclear behavior associated with septation. Also no big spores have to date been germinated. If these can be germinated, as is likely, it would be worthwhile to study the nuclear behavior during the process. The situation here is especially interesting because of the fact that the mycelium in this species is made up of uninucleate cells.

We are not yet in a position to evaluate the significance of giant spores in *Coccomyces hiemalis*. They are of interest of course as abnormalities. The observations here recorded place the cherry leaf-spot fungus among the few species, still less than ten, in which giant ascospores have been

reported. They place it in the still more limited list of normally eight-spored forms where giant spores have occasionally been found and in which convincing evidence has been adduced that more than a single nucleus is involved in the formation of each of these. We have here the first parasitic form and the first long-spored form recorded as exhibiting the phenomenon.

If this species could be shown to be heterothallic and of the type we know in *Neurospora sitophila* in which it has been demonstrated a definite segregation takes place, so that four spores of one "sexual reaction" and four of another are formed in every normal ascus, we should be able then to determine experimentally the compatibility relations of the big spores. In such a case, giant spores containing five or six nuclei, such as I have been able to observe, would surely contain nuclei of opposite "sexual reactions," and a homothallic mycelium might perhaps be expected to result when such a spore germinated, just as Moreau and Moruzi (1932a) found that in *Neurospora sitophila* certain giant spores produced a mycelium that by itself developed perithecia, although a normal sized spore in this species invariably produces a mycelium of one "sexual" reaction only.

SUMMARY

1. Origin of the asci through crozier formation is here described for *Coccomyces hiemalis*.

2. The definitive nucleus shows a protracted prophase stage in which chromatin beads are prominent.

3. The division figures show the features commonly described for nuclear divisions in asci. Four chromosomes seem to be present at equatorial plate in all three divisions.

4. Following the last division the nuclei develop prominent beaks, and the spores are delimited with the usual accompaniment of astral rays.

5. The ascospores are cut out as practically spherical bodies and only after a period of elongation and growth attain the form characteristic of mature spores in this species.

6. The occasional occurrence of asci with giant spores is reported. It has been possible to show, especially in aceto-carmine preparations, that such abnormal asci contain fewer than eight spores.

7. Evidence is presented on the basis of a cytological study that two or more of the eight nuclei present in the ascus following the third nuclear division are incorporated in each giant spore at the time it is delimited. Big spores containing from two to six nuclei are described. The possible significance of such abnormal ascospores is indicated.

I take much pleasure in expressing my indebtedness to Prof. E. M. Gilbert who suggested this study and guided it through its early stages, and especially to Dr. B. O. Dodge who sponsored the major portion of the work, during my tenure of a National Research Fellowship, and who gave most generously of his time and helpful advice. Thanks are also due Prof. R. A. Harper for examining some of the preparations, for his valuable advice on certain points, and for criticism of the manuscript. I wish in addition to express my gratitude to Prof. G. W. Keitt for his kind co-operation in providing certain materials for this study and for his sympathetic interest in the progress of the work.

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Explanation of plates

All drawings were made with the aid of an Abbe camera lucida. All except Fig. 19, Plate 29, were drawn under a Leitz 12 oil imm. lens with Leitz ocular 4. Magnification about 1400 diameters. For Fig. 19 a Zeiss 20× ocular was used; magnification obtained approximately 2900 diameters. The photomicrographs were taken at various magnifications.

Plate 29

Figs. 1–5. Croziers.

Fig. 6. Young ascus about one third grown.

Figs. 7 and 8. Uninucleate asci, showing prominent chromatin bodies in nuclei.

Fig. 9. Spireme.

Fig. 10. First division, equatorial plate.

Fig. 11. Two-nucleate ascus, nuclei showing "chromatin beads."

Fig. 12. Second division, equatorial plate.

Fig. 13. Second division, telophase; ascus showing invaginated spore-plasm.

Figs. 14 and 15. Four-nucleate stage.

Fig. 16. Third division.

Fig. 17. Eight-nucleate stage.

Fig. 18. The delimitation of the spores.

Fig. 19. Beaked nucleus and cutting-out of a spore. × about 2900.

Plate 30

Fig. 20. Spores just cut out.

Figs. 21 and 22. Stage following that in fig. 20. Spores still spherical.

Figs. 23 and 24. Two sections of same ascus. Earliest stage of elongation of ascospores. Ascus abnormally large.

Figs. 25 and 26. Early stages in elongation of ascospores.

Fig. 27. Ascus with young, very narrow, elongated spores.

Figs. 28–30. Further stages in growth and elongation of ascospores.

Fig. 31. Late stage in development of spore in uninucleate condition. The nucleus has returned to a nearly spherical shape.

Fig. 32. Cross-section of a maturing ascus, showing spore arrangement.

Fig. 33. Ascus with septate spores.

Fig. 34. Mature septate spore.

Plate 31

Fig. 35. Seven-spored ascus shortly after delimitation of spores. One spore a two-nucleate giant.

Fig. 36. Ascus with two young giant spores.

Fig. 37. Two giant spores in early stage of elongation.

Fig. 38. Two-nucleate big spore.

Fig. 39. Five-nucleate giant of atypical shape ane not full-grown.

Fig. 40. Section of ascus showing one three-nucleate giant and three normal spores.

Fig. 41. Three-nucleate spore of atypical form.

Fig. 42. Four-nucleate giant spore.

Fig. 43. Six-nucleate spore of irregular shape.

Fig. 44. Portion of an ascus showing part of a big spore with two nuclei.

Fig. 45. Portion of a giant spore showing three nuclei clumped together.

Fig. 46. Portion of a three-nucleate big spore with clumped nuclei.

Fig. 47. Abnormal ascus. A single spore just beginning to elongate, and nuclei lying free in the epiplasm.

Fig. 48. Ascus showing two small nucleoles in fusion nucleus. Note also vacuolate sporeplasm.

Plate 32

Fig. 49. Section of an unopened ascocarp showing general features. Largest asci in uninucleate condition.

Fig. 50. Section of two open apothecia. Spores elongated and nearly mature.

Fig. 51. Portions of contents of an ascocarp crushed out in aceto-carmine.

Figs. 52–54. Photomicrographs of croziers from aceto-carmine preparations.

Fig. 55. Photomicrograph of ascus showing spores in spherical stage.

Fig. 56. Photomicrographs from aceto-carmine preparations, illustrating growth and maturation of ascospores. A, B, ane C taken at same magnification. ($\times$ about 400.)

A—Ascus with spores in relatively early stage of elongation. Note condition of epiplasm.

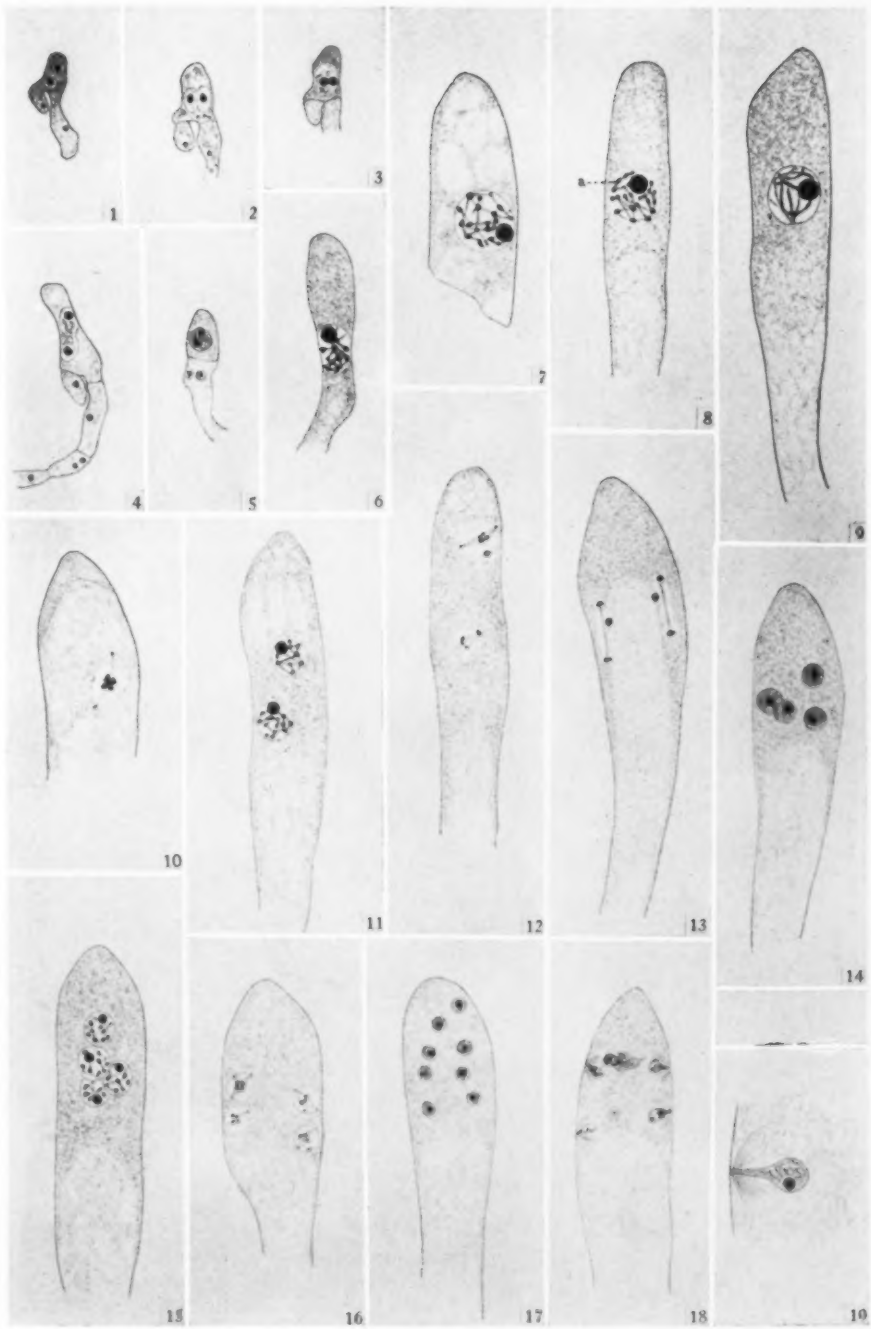
B—Ascus with spores further developed.

C—A mature spore.

Fig. 57. Abnormal ascus showing two giants, one, especially, of atypical shape.

Fig. 58. Contents of abnormal five-spored ascus with spores in process of elongation. Three giants and two normal spores.

Fig. 59. Contents of an abnormal ascus: two giant spores and four normal spores.



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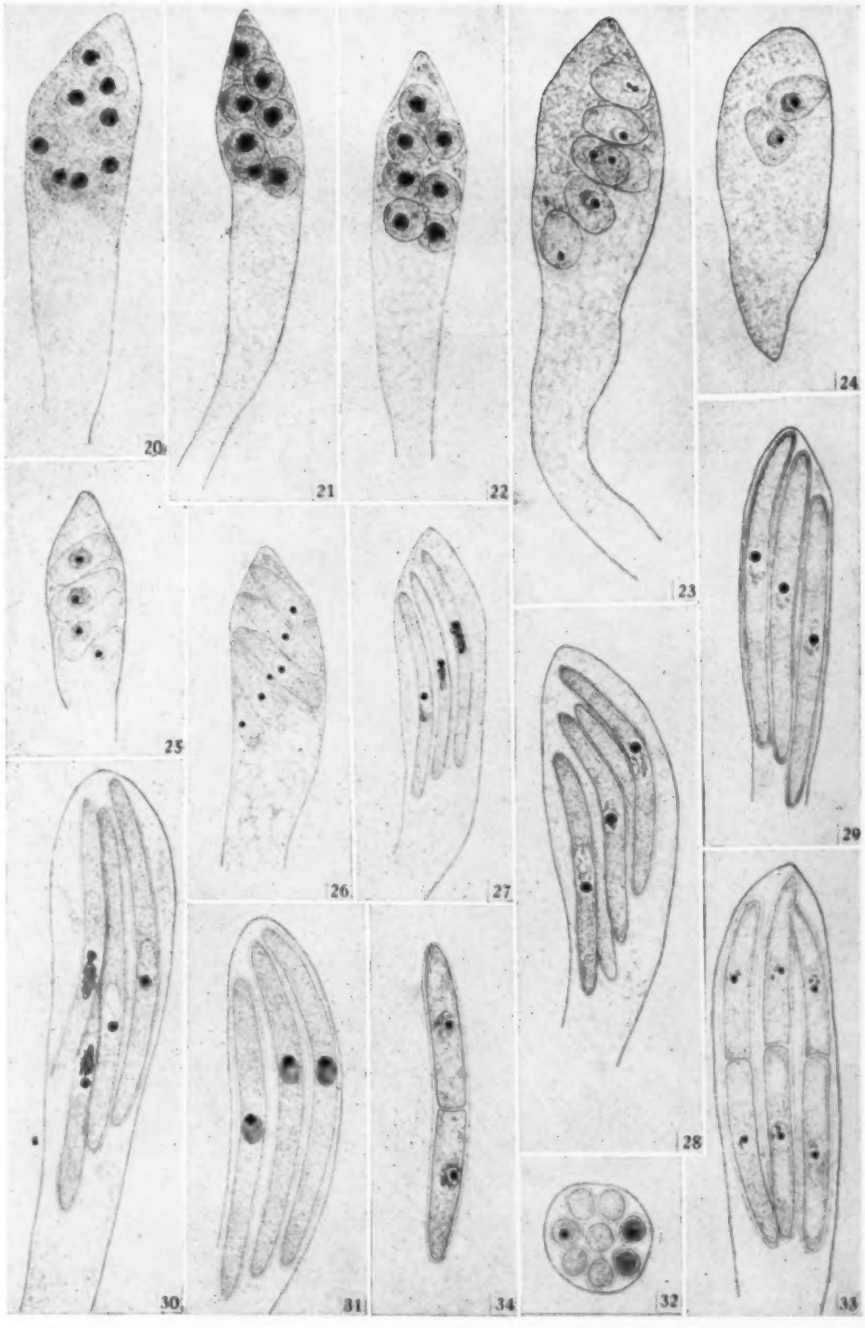

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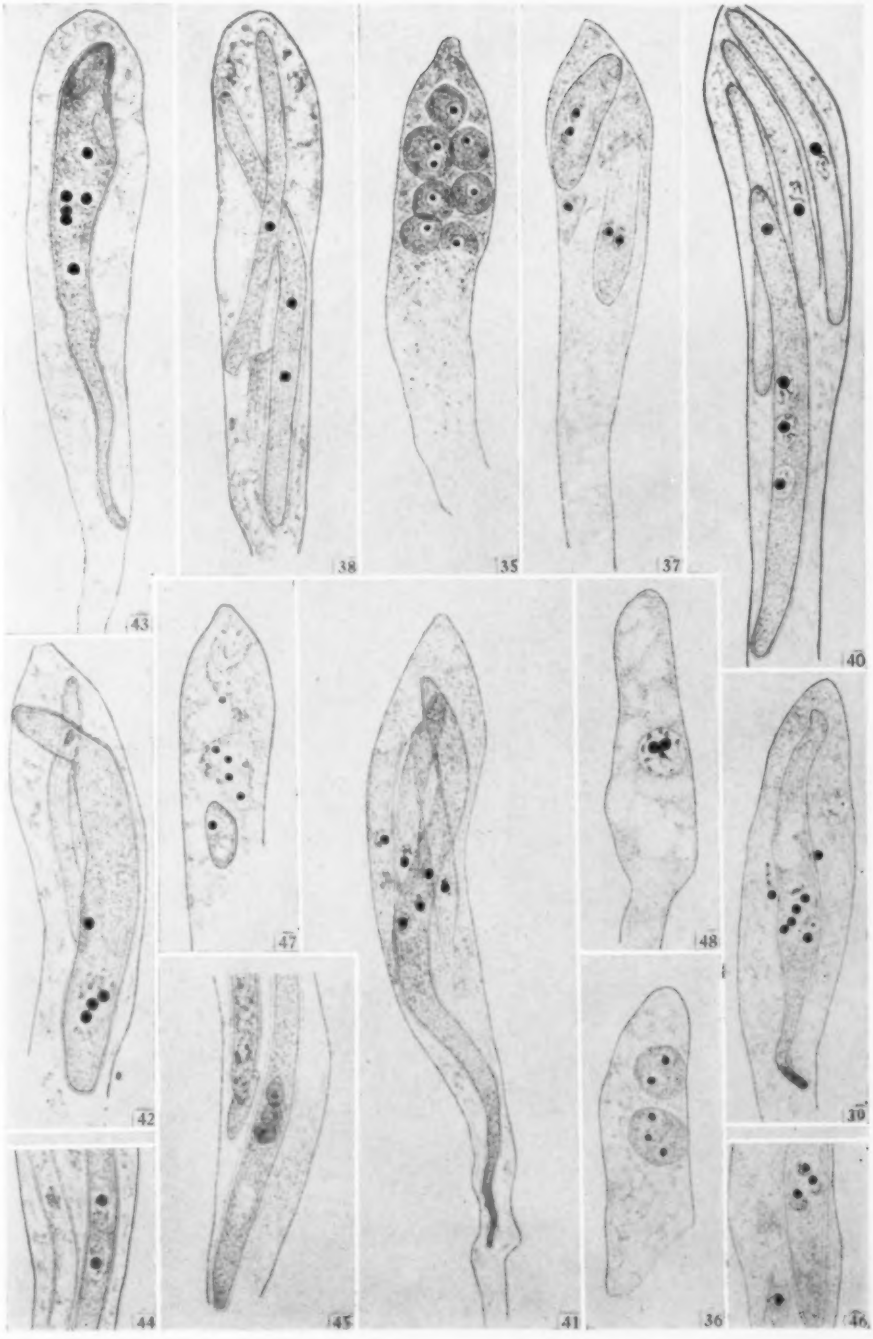

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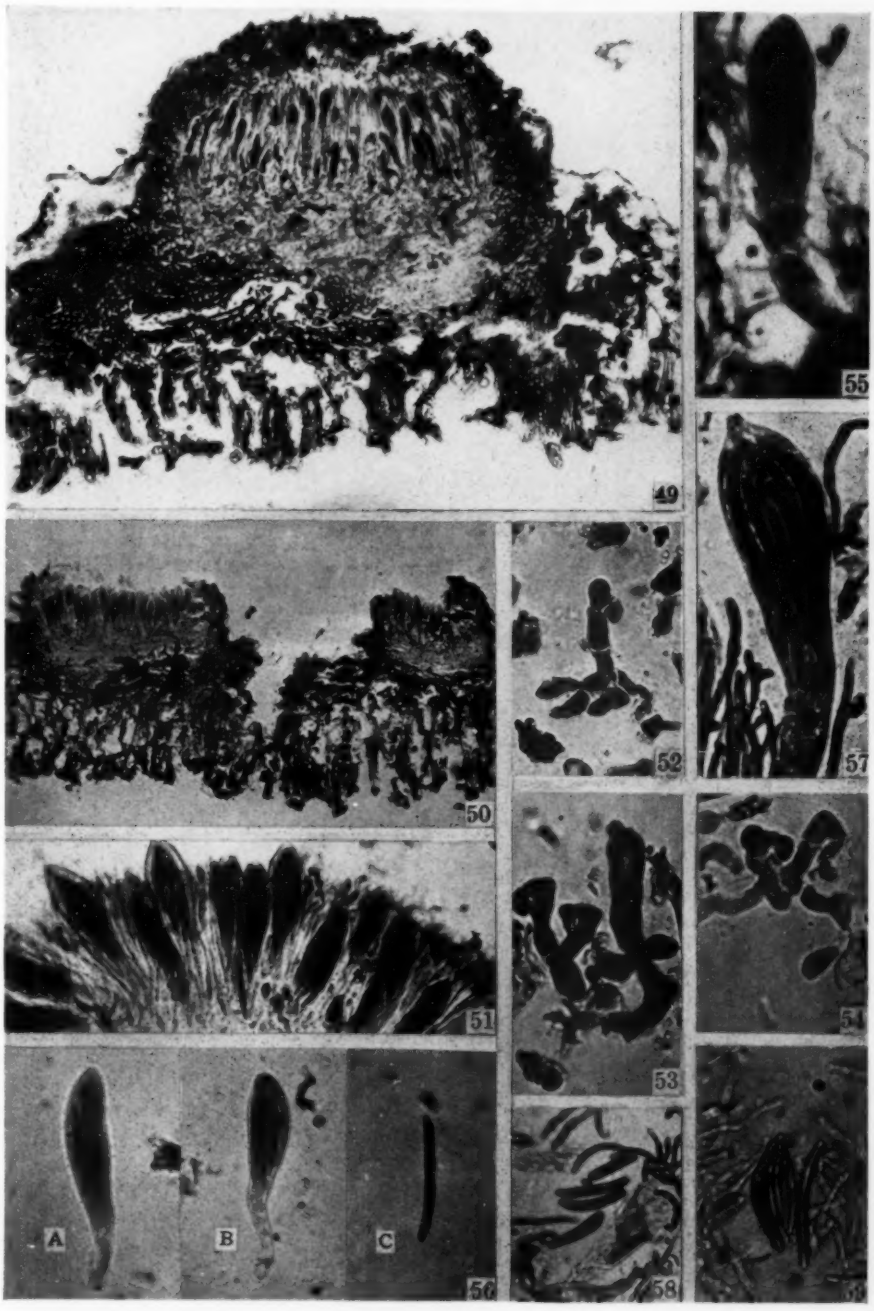

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On Poa malabarica Linnaeus

E. D. Merrill

An interesting case of interpretation of types is presented by *Poa malabarica* Linn., regarding which there may well be differences of opinion. The species has been reduced to as diverse ones as *Panicum nodosum* Kunth (*P. arnottianum* Nees) = *Hemigymnia* = *Ottochloa;* by an error in identification to *Centotheca lappacea* Desv. = *C. latifolia* (Osbeck) Trin.; and to *Diplachne fusca* Beauv. The case seems to be worthy of more extended consideration than has been given it. Munro (Jour. Linn. Soc. Bot. **6:** 43. 1862) stated that the specimen of *Poa malabarica* in the Linnaean herbarium is *Panicum arnottianum* Nees. This was noted by me (Philip. Journ. Sci. Bot. **4:** 248. 1909) when I transferred the specific name to *Panicum* as *P. malabaricum* (Linn.) Merr., on the assumption that this specimen was the actual type. At this time, on the basis of a rough tracing of Rheede's illustration, I considered that his plate of *Tsiama-pulu* represented the same species as the specimen in the Linnaean herbarium that had been examined by Munro. This is not the case, however, as noted by Stapf (in Prain Fl. Trop. Afr. **9:** 743. 1920) who there proposed the generic name *Hemigymnia* to include *Panicum multinode* Presl = *P. nodosum* Kunth and *P. arnottianum* Nees. Hooker f. referred Rheede's illustration, cited by Linnaeus in the original description of *Poa malabarica* Linn. to *Diplachne fusca* Beauv. and Stapf thus accepts this: "What Rheede's plate represents may be doubtful but I would suggest that it was drawn from a specimen of *Diplachne fusca*." It unquestionably represents Beauvois' species.

In 1930 Henrard (Meded. Rijks Herb. Leiden **61:** 12. 1930) after examining the specimen of *Poa malabarica* Linn. in the Linnaean herbarium, concluded that it represented a species distinct from both *Panicum nodosum* Kunth and *P. arnottianum* Nees, and transferred the specific name to *Hemigymnia* as *H. malabarica* (Linn.) Henrard for a species known only from southeastern China and Indo-China. A year later Dandy (Jour. Bot. **69:** 54. 1931) proposed the new generic name *Ottochloa* for *Hemigymnia* Stapf, non Griff., with the binomial *Ottochloa malabarica* (Linn.) Dandy for the southeastern Asiatic form. Stapf, Henrard and Dandy all assumed that the actual specimen in the Linnaean herbarium, one collected by Osbeck near Canton, China, was the actual type of *Poa malabarica* Linn. I do not accept this interpretation as, even with Linnaeus' wide concept of geographic areas as appertaining to "India," I consider it illogical to typify a species bearing the name *malabarica* by a specimen collected in southeastern China, and a form that does not occur in Malabar,

or even in India, and one that does not conform to the characters given by Linnaeus.

The original Linnaean description of *Poa malabarica* is as follows:

"Poa paniculae ramis simplicissimis, floribus sessilibus, seminibus distantibus, culmo repente. Tsiama-pulu *Rheed. mal.* 12. *p.* 83. *t.* 45. *Habitat in* Indiae *arenosis.*"

It may be noted that Linnaeus took his specific name, all the characters, except possibly "culmo repente," and the habitat from Rheede who states as to the habitat: "Planta arenosa gaudens solo," and as to the spikelets "spicae . . . oblongae, cuspidatae . . . quatuor constantes foliolis cuspidatis, in singulis semen includitur unicum." These characters are not those of *Panicum* (*Hemigymnia*, *Ottochloa*), but apply to *Diplachne*, and the illustration clearly represents *Diplachne;* nor does the Linnaean phrase "seminibus distantibus" apply to *Panicum*, while the habitat cited is not that of *Panicum nodosum*. Yet Stapf states that this description was based on the specimen in the Linnaean herbarium, not on Rheede's illustration. He considers that Linnaeus' quotation of the reference to Rheede is of little importance in this instance and explains the habitat "in Indiae arenosis" by the loose way in which the term India was used in those days or as a consequence of Linnaeus' mistaken identification of the plant of Rheede.

In tracing the history of the specimen in the Linnaean herbarium, which was in the herbarium in 1753, when the first edition of the Species Plantarum was published and which was named *Poa malabarica* by Linnaeus himself, it is found that this was collected by Osbeck in the vicinity of Canton, China, December 17, 1751, as recorded by Osbeck himself. He reached Sweden on his return trip to Europe on June 26, 1752. It is probable that his botanical material was delivered to Linnaeus shortly after he reached home, for some species based on Osbeck's specimens are included in the first edition of the Species Plantarum (1753).

It is clear that in June 1752 the manuscript of the Species Plantarum was well advanced and that these Osbeck references were interpolated in the manuscript or in the text. It seems also safe to assume that *the entire original basis of Poa malabarica* Linn., at least as to the original manuscript, was the illustration and description cited from Rheede's Hortus Malabaricus; that the erroneous identification of Osbeck's specimen as representing *Poa malabarica* was hurriedly done; and that perhaps the phrase "culmo repente" was added from the actual specimen. In view of these circumstances, and particularly in view of the Linnaean description, and the fact that his concept of *Poa* included *Eragrostis*, but nothing ap-

proaching *Panicum*, I do not accept the named specimen in the Linnaean herbarium as the actual type of *Poa malabarica*, but interpret the species wholly from Rheede's illustration and description; the specimen merely represents an erroneous identification on the part of Linnaeus. That he noted the error is evidenced by the fact that in repeating the description, Species Plantarum ed. 2, 100. 1762, he eliminated the reference to Rheede but did not otherwise modify it, so this description does not apply to the *Panicum* (*Hemigymnia*, *Ottochloa*), even the "seminibus distantibus" remaining as in the original. Neither here nor in the original description does Linnaeus cite the Osbeck specimen, or China as a habitat, nor is there any indication in the description, except possibly the "culmo repente," that it was based on an actual specimen. The case might be disposed of under the rule that a description based on a mixture of two or more species is invalid, but I personally prefer to interpret this Linnaean species on the basis of the description and illustration cited by him, ignoring the specimen as erroneously named. The partial synonymy would then be as follows:

Diplachne malabarica (Linn.) comb. nov.

Poa malabarica Linn. Sp. Pl. 69. 1753, quoad syn. Rheede, excl. spec. in herb. Linn.
Festuca fusca Linn. Fl. Palaest. 13. 1756, *nomen nudum*, Amoen. Acad. **4**: 450. 1759, *nomen nudum*, Syst. ed. 10, 876. 1759, Sp. Pl. 109. 1762.
Bromus polystachios Forsk. Fl. Aeg.-Arab. 23. 1775.
Festuca indica Retz. Obs. **4**: 21. 1786.
Triodia ambigua R. Br. Prodr. 183. 1810.
Diplachne fusca Beauv. Agrost. 163. 1812.
Poa procera Roxb. Fl. Ind. **1**: 334. 1820.
Diplachne indica Spreng. Syst. **1**: 351. 1825.
Leptochloa? fusca Kunth Distr. Méth. Gram. 91. 1829.
Uralepis fusca Steud. Syn. Gram. 247. 1854.
Uralepis drummondii Steud. l. c. 247. 1854.
Eragrostis procera Steud. op. cit. 266. 1854.

Diplachne polystachya Backer in Bull. Jard. Bot. Buitenz. III. **2**: 325. 1920.

Backer notes (Bull. Jard. Bot. Buitenz. III. **2**: 325. 1920), that *Festuca fusca* Linn. (Sp. Pl. ed. 2, 109. 1762) the name bringing synonym of *Diplachne fusca* Beauv., was described from a Palestine specimen as having a decompound panicle with 16- to 24-flowered spikelets about an inch long and because these are not characters of *Diplachne fusca* Beauv. he abandoned the Linnaean specific name and accepted for the common and widely distributed grass currently referred to *Diplachne fusca* (Linn.) Beauv. the binomial *Diplachne polystachya* Backer, based on *Bromus*

polystachios Forsk. (1775). In *Diplachne fusca* Beauv. as currently interpreted the spikelets are usually less than 1 cm long and bear from 4 to 16 florets. At my request Mr. J. E. Dandy of the British Museum, Natural History, examined the Linnaean type and reports as follows:

"I have examined Linnaeus's type-specimen of *Festuca fusca* at the Linnean Herbarium, and am of the opinion that it is conspecific with the grass currently passing as *Diplachne fusca*. Linnaeus's description, Sp. Pl. ed. 2, is misleading. I counted the florets in a few spikelets of the type and found 8–11 florets to a spikelet. Linnaeus stated that there were 16–24, but I suspect that he counted the florets of two spikelets which happened to be lying end to end; at any rate he certainly miscounted them. The type-sheet bears the written sign ⊖ which means that the specimen was collected by F. Hasselquist (in Palestine). The epithet *fusca* is written at the bottom of the sheet. Incidentally the name *F. fusca* was first published (as a nomen nudum) by Linnaeus in 1756 and a description first appeared in 1759. The full reference is as follows: *Festuca fusca* L., Fl. Palaest. 13, nomen nudum (1756); Amoen. Acad. **4:** 450, 1759, nomen nudum: Syst. Nat. Ed. 10, **2:** 876. (1759); Sp. Pl. Ed. 2, **1:** 109. (1762)."

Some may object to this interpretation because Rheede's rather crude figure shows distant obtuse glumes, more like those of some species of *Eragrostis;* yet his description calls for cuspidate glumes, and while the spikelets are described as having four "foliolis" the figure actually shows 5 to 9 glumes. Hooker f. (Fl. Brit. Ind. **7:** 329. 1897) and in Trimen (Fl. Ceyl. **5:** 300. 1900) reduced Rheede's illustration Hort. Malabar. **12:** *pl. 45*, to *Diplachne fusca* Beauv. and I accept this as correct, yet in so doing it involves the new combination made above.

As noted above, Stapf proposed the new generic name *Hemigymnia* in 1920 to include *Panicum multinode* Presl=*P. nodosum* Kunth, and *P. arnottianum* Nees. On the basis that this name was invalidated by the earlier *Hemigymnia* Griff., Dandy proposed the new name *Ottochloa* in 1931. If a distinct genus be represented, Dandy's name should be accepted. The difference between *Ottochloa* (*Hemigymnia*) and *Panicum* are so slight that I see little reason for maintaining this small group as generally distinct and accordingly here consider the species under *Panicum* in my present discussion of certain nomenclatural problems involved.

Stapf, followed by E. G. and A. Camus, recognized *Hemigymnia multinodis* Stapf and *H. arnottiana* Stapf as representing distinct species. When I erroneously accepted the Linnaean name under *Panicum malabaricum*, I referred to it the large form with ample panicles, retaining *Panicum nodosum* Kunth, the common Philippine plant with rather small panicles, as a distinct species. The two species, *Panicum "malabaricum"* and *P.*

nodosum, were recognized in my Enum. Philip. Fl. Pl. **1**: 65. 1923. I do not detect any sufficiently well marked constant differences between the typical Indian *Panicum arnottianum* Nees and the Philippine *Panicum nodosum* Kunth, as there seem to be all intergrades between the large- and small-panicled forms. The differences indicated by E. G. and A. Camus between *Hemigymnia arnottiana* Stapf and *H. multinodis* Stapf are wholly differences in size of the panicles and slight differences in the disposition of the spikelets, but these do not appear to me to be constant; there seem to be no differences in the size and details of the spikelets. Backer recognizes but a single species as occurring in Java, and I am of the opinion that he is correct. The differences in the size of the plants and of their panicles seem to be largely due to differences in habitat. The synonymy as I understand it is as follows:

Panicum nodosum Kunth Enum. **1**: 97. 1833 (based on *Panicum multinode* Presl); Hook. f. Fl. Brit. Ind. **7**: 43. 1897.
Panicum multinode Presl Rel. Haenk. **1**: 303., 1828, non Lam.
Panicum violaceum Llanos Fragm. Pl. Filip. 42. 1851.
Panicum arnottianum Nees in Steud. Pl. Glum. **1**: 59. 1854.
Panicum ouonbiense Balansa in Jour. de Bot. **4**: 142. 1890.
Hemigymnia multinodis Stapf in Prain Fl. Trop. Afr. **9**: 742. 1920; E. G. & A. Camus in Lecomte Fl. Gén. Indo-Chine **7**: 454. 1922.
Hemigymnia arnottiana Stapf l. c., E. G. &. A. Camus op. cit. 455.
Panicum malabaricum Merr. in Philip. Jour. Sci. Bot. **4**: 248. 1909; Backer Handb. Fl. Java **2**: 159. 1928, non *Poa malabarica* Linn.

This species is widely distributed in tropical Africa, tropical Asia, Malaysia and the Philippines.

The form occurring in Kwangtung Province, China, and in Indo-China, is considered by Henrard to represent a species distinct from both *Panicum nodosum* Kunth and *P. arnottianum* Nees. It has somewhat smaller spikelets than these, which I consider to represent a single species, usually about 2 mm. long, but apparently varying from 1.5 mm. to 2.5 mm. in length. In *Panicum nodosum* Kunth (*P. arnottianum* Nees) they are 3 mm. long. The chief spikelet differences appear to be in the size, as the glume characters seem to be rather remarkably uniform. I do not recognize *Ottochloa* (*Hemigymnia*) as generically distinct from *Panicum*, and, under the circumstances, prefer to retain Balansa's varietal name, rather than to propose a new binomial for the southeastern Asiatic form. *Panicum nodosum* Kunth var. *micranthum* Balansa is the form that is represented in the Linnaean herbarium by an Osbeck specimen from the vicinity of Canton named by Linnaeus *Poa malabarica*. The application of this specific name is discussed under *Diplachne malabarica* (Linn.) Merr. The synonymy of this small-spikeleted form is as follows:

Panicum nodosum Kunth var. **micranthum** Balansa in Jour. de Bot. **4:** 142. 1890.

Poa malabarica herb. Linn., non *Poa malabarica* Linn. Sp. Pl. 69. 1753.

Hemigymnia arnottiana Stapf var. *micrantha* A. Camus in Lecomte Fl. Gén. Indo-Chine **7:** 455. 1922.

Hemigymnia malabarica Henrard in Meded. Rijks Herb. Leiden **61:** 12. 1930, non *Poa malabarica* Linn.

Ottochloa malabarica Dandy in Jour. Bot. **69:** 54. 1931, non *Poa malabarica* Linn.

Panicum nodosum Hitchc. in Lingnan Sci. Jour. **7:** 219. 1931, non Kunth.

A form only known from Kwangtung Province, China, and Indo-China.

Hooker f. (Fl. Brit. Ind. **7:** 332. 1897) cites as a synonym of *Centotheca lappacea* Desv. "*P*[*oa*] *malabarica, Linn. Sp. Pl.* 69; *Burm. Fl. Ind.* 27, *t. 11, f. 2*," on the basis of which I erroneously transferred the above specific name to *Centotheca* as *C. malabarica* (Linn.) Merr. in 1906. Hooker's error was in the citation of the Linnaean reference, as *Poa malabarica* Linn. Sp. Pl. 69. 1753 has nothing to do with *Centotheca*, but *Poa malabarica* Burm. f. Fl. Ind. 27. *pl. 11, f. 2.* 1768, is clearly the same as *Centotheca lappacea* (Linn.) Desv. = *C. latifolia* (Osbeck) Trin. As the Linnaean binomial *Poa malabarica* has thus been erroneously associated with *Centotheca* it is briefly discussed here. No attempt has been made to compile the very numerous synonyms, of which Hooker f. cites no less than 22. Those given below are chiefly those necessary to explain the acceptance of the specific name *latifolia*, with several additions to Hooker's list. There are probably over 30 synonyms for this very common, characteristic, and widely distributed species.

Centotheca latifolia (Osbeck) Trin. Fund. Agrost. 141. 1820.

Holcus latifolius Osbeck Dagbok Ostind. Resa 247. 1757; Linn. Syst. ed. 10, 1305. 1759.

Poa latifolia Forst. f. Prodr. 8. 1786.

Poa malabarica Burm. f. Fl. Ind. 27. *pl. 11, f. 2.* 1768, non Linn.

Cenchrus lappaceus Linn. Sp. Pl. ed. 2, 1488. 1763.

Centotheca lappacea Desv. in Nuov. Bull. Soc. Philom. **2:** 189. 1810.

Melica philippinensis Llanos Frag. Pl. Filip. 44. 1851.

Centotheca malabarica Merr. in Philip. Journ. Sci. Suppl. **1:** 385. 1906; Koord. Exkursionsfl. Java **1:** 159. 1911, non *Poa malabarica* Linn.

Anthoxanthum pulcherrimum Lour. Fl. Cochinch. 29. 1790.

It may be noted that Trinius in publishing the binomial *Centotheca latifolia* based it on *Cenchrus lappaceus* Linn.; "*Centotheca latifolia* (*Cenchrus lappaceus* L.)," but later (Mém. Acad. St. Petersb. Math. Phys. Nat. **1:** 358. 1830) under *Uniola lappacea* Trin. = *Centotheca lappacea* Trin. = *C. latifolia* Trin., he cites *Holcus latifolius* Linn. as a synonym. Linnaeus in 1759 cites Osbeck's references but does not credit the binomial to Osbeck, yet Osbeck's binomial antedates Linnaeus' use of it by two years.

Sex and chromosomes in plants

CECIL YAMPOLSKY

(WITH 16 TEXT FIGURES)

If an increasing number of corroborative evidences is a measure of the validity of an assumption, then the existence of the sex chromosome in plants is an established fact and the problem of sex determination is no longer a problem from the Mendelian standpoint; it has been solved. Sex determination in plants involves merely an extension of the concept that explains sex in animals. Lindsay (1930) lists forty-three angiosperm forms in which heterochromosomes have been found and that does not include the eight hepatics in which heterochromosomes are present. Since then more forms have been added to the list.

Ever since Allen (1917) announced the presence of sex chromosomes in the hepatic *Sphaerocarpos Donnellii*, there has been a steady gain in the number of plants that are shown to have a correlation between sex expression and a specific chromosome. On the other hand, negative evidence, both among angiosperms and hepatics where no obvious correlation exists between sex forms and a special chromosome, has accumulated.

The cell concept held sway for three quarters of a century. In its time old values were brushed aside and new values established. Since the beginning of the twentieth century the supremacy of the cell in biologic thought has had a contender in the form of the newer genetics, Mendelism. Both the Galtonian and the Mendelian analyses of genetic phenomena are mathematical. They deal with populations and involve a statistical approach towards biologic problems. Parents and children are compared numerically; all morphological and physiological attributes of the organism are in reality conceived in terms of units and as numerical values even when the claim is made of a distinction between qualitative and quantitative characters. Hybrid and non-hybrid, heterozygous and homozygous! Sex has its explanation in the mating of a homozygous individual with a heterozygous individual. What clearer parallelism could have been conceived to account for the one to one ratio? Segregation of genes! A magic formula in which a series of complex phenomena find their simplification.

In recent years we have witnessed an alliance between a discipline like Mendelism with its mathematical ideology, a discipline where the unit one is not an individual but a number, and a discipline such as cytology which deals with actual individuals and more specifically with the ultimate units of the organism, the cells. From this alliance hybrid offspring have arisen, not with blended inheritance, but with conflicting developmental tendencies. At the present moment cytology accepts all the pro-

nouncements of the geneticist. When the mathematician-biologist gets into difficulties with his calculations the cytologist extricates him by directing his attention to the multiplicity of possible structural elements in the nucleus, viz. maternal and paternal chromosomes, serial arrangement of genes, chromatin granules in pairs, parasynapsis, chiasmatypy, four-strand crossing-over, non-disjunction, fragmentation of chromosomes, polyploids, diploids, triploids, tetraploids, and not to forget sex chromosomes or heterochromosomes, and bids him take his choice. Explanations come from one part of the cell—the nucleus, and particularly from a special part of the nucleus, the chromosome. What does a philosopher think of such a marriage of convenience between genetics and cytology? Truly an eclectic approach to the solution of the problem of life! The geneticist thinks in terms of summations and subtractions and arrives at his conclusions through the manipulation of irreducible non-visible entities, genes, and the cytologist, abandoning the building stone, the cell with its self-perpetuating organization, is led to interpret with greater and greater freedom the very difficult data as to the mating of colloidal germ plasms in terms of the additions and subtractions of genetical experimentation.

Alternative sex inheritance can be described in terms of heterochromosomes providing opposite sexes are in question. In the plant kingdom, dioecism is wide-spread but it is not the preponderant condition. The large array of sex forms in the phanerogamic flora should make one pause before postulating an all-embracing scheme to explain sex in plants. Hermaphrodite, dioecious, monoecious, andromonoecious, gynomonoecious, androdioecious, gynodioecious, polygamous, polyoecious, and combinations of the various groups give over forty sex categories in the flowering plants not including the quite independent but equally demonstrable data on compatibilities. If our knowledge of evolutionary trends were sufficiently sure to allow us to say with certainty that dioecism is a derived condition and is the most recent sex state, then we would be justified perhaps in correlating this separation of sexes with definite chromosomes in the gamete cells. A survey of the distribution of the sexes (Yampolsky, 1922) fails to show that dioecism is the end goal of sex expression in the various families. Neither the monocots nor the dicots show orthodox leanings towards any one sex category. The currents of sex differentiation in the families of plants may run parallel; they may cross; they may run upstream or down-stream. From the heights they look like a patchwork quilt of many hues and designs. Why should one sex form, dioecism, be correlated with the presence or absence of a particular chromosome? Is hermaphroditism less of a sex condition? What about monoecism and the other sex categories? Cytology has failed to yield evidence which would

tend to show a correlation between chromosome number, size, or form and phylogeny (Farmer and Digby, 1914). Why should dioecious plants have been singled out for such a correlation? Why should a quantitative difference in chromosomes effect morphological differences in males and females? Why should there not be a similar correlation in all forms of sex expressions? Why should some dioecious plants show no visible correlation? Certainly the change from a non-sexual sporophyte to one that produces eggs or sperms or both is sufficiently profound, since climax structures—flowers, are achieved. We have no such evidence. That changes in the germ plasm must have occurred no one can deny. We do not know how the modification in the protoplasm was brought about.

The presence of sex chromosomes in hepatics is not comparable with the presence of such bodies in flowering plants. In *Sphaerocarpos Donnellii*, *S. texanus*, *S. terrestris*, *Riella helicophylla*, *Pellia Fabbroniana*, *P. Neesiana*, *Moerckia hibernica*, and in *Makinoa crista*, sex determination is associated with the reduction divisions. Sex is expressed when maternal and paternal hereditary complements separate. The union of sex chromosomes in the forms listed, results in a neutral sporophyte. That sporophyte contains x and y chromosomes and it exhibits no morphological expression correlated with those chromosomes. What becomes in this case of the concept that sex chromosomes operating in a common medium give rise to one or the other sex depending upon quantitative or qualitative equality or difference? If sex chromosomes have any significance in hepatics they suggest the fact that *sex expresses itself at the end of a cycle*. In these forms it is when cells throw off the yoke of duality that we have the fullest manifestation of sex. Fertilization yokes the two gametes and robs them of their independence.

The gametophyte expression in liverworts, in mosses, and in ferns is the expression of an independent haploid generation with but one set of chromosomes. On the assumption that sex chromosomes operate independently in such gametophytes there should be no possibility of sex reversal. In spite of Allen's (1932) pronouncement about the strict unisexuality in certain species of *Sphaerocarpos*, that the plants arising from the spores from the beginning are predestined to be male or female and no change in conditions may induce intersexuality or sex reversal, the case for obligate maleness or femaleness is weakened by his own statement that the genus *Marchantia* includes also hermaphrodite species.

Gertraud Haupt's work (1933) on *Marchantia grisea* has just appeared. It forms an important link in the chain of observations on the liverworts. This liverwort is androdioecious since only hermaphrodite and male plants exist. The male plant contains nine chromosomes, four paired ones

and one unpaired. The male sex organs of the hermaphrodite are borne on separate branches, so also are the female sex organs. Some branches contain both male and female elements. The cells of the hermaphrodite plant contain ten chromosomes. The female sex organs contain ten chromosomes, one a very small one called the *z* chromosome. The male sex organs on the hermaphrodite plant contain nine chromosomes. In the formation of the male sex organs the *z* chromosome is lost. Fertilization gives to the sporophyte nine and nine and one (*z*) chromosomes, nineteen in all. The *z* chromosome is responsible for the female sex; the unpaired chromosome is responsible for the male sex. In the sporophyte the two male chromosomes pair; the female sex chromosome alone remains unpaired.

The literature on intersexuality in liverworts is meager but as few as the cases may be they point to a fluidity of sex expression. Taylor (1836) described an androgynous gametophyte in *Dumortiera irrigua*. Townsend (1899) found archegonia on the male thallus of *Preissia commutata*. Ernst (1907) found androgynous receptacles in *Dumortiera velutina*. Cutting (1910) found antheridia on the archegoniophore of *Marchantia polymorpha*. Limprecht (1890) found intersexual stages in *Jungermannia Kaureni* and *Cephalozia Gottschei*.

In the dioecious mosses, in dioecious fern prothallia, and in heterosporous ferns mixed sexuality occurs (Yampolsky, 1919). Whatever the determining factors that produced gametophytes of one sex may have been, they are not absolute in their effects because transitions from one to the other sex have been observed.

Sphaerocarpos Donnellii (Allen, 1919) and *Riccia Curtisii* (MacAllister, 1928) show an interesting parallelism since the spores are held in tetrads and since also upon germination of those spores there appears to be an equal distribution of males and females. This would indicate a similarity in the mechanism of sex determination. A cytological examination of *Riccia* shows no such similarity.

Contrasting the hepatics with sex chromosomes reported with those in which no sex chromosomes have been observed we may well ask ourselves what the significance of the sex chromosome is. We cannot deny its presence but its absence does not suppress sex. In *Riccia*, in *Marchantia*, in *Conocephalum*, in *Riccardia*, in *Blasia*, in *Diplophyllum*, in *Scapania*, sex expression is as patent and as evident as in *Sphaerocarpos*, in *Riella*, in *Pellia*, in *Moerckia* and in *Makinoa*. There is no direct evidence that *x* and *y* chromosomes in hepatics control sex. *If the x and y chromosomes have any significance in hepatics* it is an indirect one; they are found to accompany sex but apparently not to control sex determination.

In approaching the problem of sex chromosomes in flowering plants it

is with the realization that the task is a difficult one. It was a foregone conclusion that when genetical data and chromosomes became interrelated in the minds of investigators, sex would find its explanation in chromosomal structure too. That such is the case is an accepted fact. The Mendelian concept of sex demonstrated in animals and accepted by students of sex in plants received its final support in the discovery of sex chromosomes in plants. And curiously enough its discovery in the liverworts complicated rather than clarified the situation. In the liverworts sex is determined at the reduction division; the plants resulting from the haploid spores do not have their counterpart in the animal kingdom. The gametes of the animal, egg and sperm, contain the sex chromosomes but those gametes are quite limited in their capacity for development; they have not the power of self-propagation; they die unless they mate. From such a mating individuals arise male and female; sex is determined at fertilization. Sex is determined when duality is established. In the liverworts and their like sex appears when duality is broken down. A comparable situation? Not at all! The explanation that holds for sex in the liverworts does not hold for sex in animals nor for sex in flowering plants. Sex in flowering plants it is claimed, is established at fertilization just as it is in animals and by the same kind of mechanism. A curious paradox! In the case of the liverworts, mosses and ferns, sex is established at reduction division. In the dioecious flowering plants the reduction division dissolves the sexual state. In liverworts fertilization results in a non-sexual sporophyte, and x and y chromosomes do not influence morphological expression. In flowering plants fertilization results in a sexual sporophyte and x and y chromosomes do influence morphological expression. There is no correlation between sex determination in flowering plants and sex determination in the liverworts. If sex chromosomes in dioecious flowering plants are determiners of sex the explanation must be sought in the parallel phenomenon in animals.

To deny the existence of bodies in the cell that behave differently from the mass of chromosomes would be not to believe what the eye sees. Such bodies are demonstrable and their behavior can be traced as much as behavior stages in coagulated protoplasm can be traced. Knowing the nature of the sex to be investigated and finding structures in the sex cells that lend support to digamety, it takes no subtle reasoning to correlate the two. The reasoning is as follows: paternal and maternal chromosomes pair, equal with equal, male chromosome with female chromosome. If male and female chromosomes differ in one or more respects, either from one another or from the autosomes, that difference will stand out when the two pair prior to reduction division.

Such cytological evidence would be unassailable if somewhat analogous

phenomena were not observed in hermaphrodite plants that undergo what is commonly called abnormal meiosis—whether the abnormality is due to physiological disturbances other than hybridity, or is due to disturbances in hybrids as a result of various incompatibilities. I have examined a large number of such cytological figures and it would have been easy to make out a case for gametic heterozygosity in many of them. I have before me the work of Sinoto (1929) in which he describes sex chromosomes. From the point of view of the classical cytologist, the inadequacy and the crudeness of the figures accompanying the observations would weaken the author's evidence. Yet it is accepted and quoted.

All the evidence to support sex and sex chromosomes is circumstantial. Is that not also true for the evidence that links cell form and function with chromosomes? Have not the defenders of the sanctity of the sex chromosomes begun to feel the need of accessory hypotheses? The reason is that the conception of sex as an alternative inheritance is untenable. Intersexualism is no longer the game of the teratologist. It is a widespread condition. The intersexual forms bridge the gap between male and female. But where are the bridging chromosomes between x and y ?

It is an obvious fallacy to predicate that a part is greater than the whole. Yet in practice, cytology has subscribed to that principle. And the greatest supporters of that fallacy have been those who have read into the chromosomes all the characteristics of the adult individual. At best cytological evidence is circumstantial. The technique that the student of the cell has evolved yields him clues from which he may reconstruct physiological processes. The very stages in mitotic division of which we have but an incomplete knowledge are but the parts of a chain visible to the eye. We then reconstruct in our mind the steps that cannot be seen. When a cell is activated towards division we cannot visualize the urge. Yet that 'urge' makes itself felt in all parts of the cell; in the cell wall, in the cytoplasm, and in the nucleus. Our attention has been focused upon the activities of a part of the nucleus and the dramatic qualities of the performers have made us forget the silent forces that pull the strings that make the actors act. The pattern of nuclear and cell division is universal, the discrete bodies, chromosomes, move through space, now they are together, now they are separated perhaps to continue their activities. The chromosomes, visible to the eye, have caught the fancy of the world; the actors make the play.

The sex chromosome has been singled out for an especially important rôle and to it are attributed far-reaching properties. If we take such a chromosome and place it side by side with the morphological and physiological characteristics bound up with a particular sex, sex-linked, we say,

we find strange contrasts. The sex-chromosome may be directly responsible for the primary and secondary sex expressions. I have examined the chromosomes in the male plant of *Mercurialis annua* (Yampolsky, 1925) and I have followed some of the steps from the undifferentiated pollen mother cells to the tetrads where the final distribution of chromosomal material has been achieved. And from those observations I was unable to single out a chromosome which seemed to bear the burden of sex determination. I found no correlation between one chromosome and the distinguishing characteristics of the male plant. Granting for the moment that one of the eight chromosomes is a sex chromosome and granting also for the moment that the male plant possesses secondary sex characters, we can diagram the relationship between the sex chromosomes and the visible secondary sex characters thus:

Sex chromosome reponsible for:
- inflorescence—spike
- color of plant—light green
- leaves—longer than in female
- petiole—longer than in female
- internodes—longer than in female
- angle of branching—45°—a lesser angle than in female
- branches—less ramified than in female
- growth—less vigorous than female
- individual flower
  - calyx
  - stamens
    - anther, pollen grains
    - filament

What holds true for the male determining chromosome must equally hold true for the sex chromosome and secondary sex characters in the female, thus:

Sex chromosomes in the female responsible for:
- inflorescence—sessile
- color of plant—dark green
- leaves—shorter than in male
- petiole—shorter than in male
- internodes—shorter than in male
- angle of branching—90°—greater than in male
- branches—more ramified than in male
- growth—more vigorous than in male
- individual flowers
  - calyx
  - ovary
  - ovule
  - stigma
  - style
  - embryo sac

The other characteristics of the plant, male or female, owe their expression to the so-called autosomes. The absence of a definite correlation

between any one chromosome and morphological expression became apparent from a study of the characters that are sex limited. The evidence gathered (Yampolsky, 1930) shows that all the characteristics of one sex may have their counterpart in the plant of the opposite sex; that leaf, petiole, internodes, angle of branching, vigor of growth, etc., do not behave as units but show a great range of variability grading from one extreme into the other. Sex intergradation in *Mercurialis annua* is widespread without attendant sterility. We have then the curious condition of one side of an equation which is constant being equal to the other side which is variable. The equation in which a sex chromosome in the male gamete is responsible for, or is equal to, primary and secondary sex characteristics is no longer an equation when the variability of one side is not counterbalanced by an equal variability in the sex chromosome. But, those who describe sex chromosomes recognize them because of their constancy and do not claim variability for them. Variability in sex expression previously considered sex-linked has now been explained in terms of autosomal influences.

The fact nevertheless remains that sex in dioecious plants is explained on the assumption that one of the parents is heterozygous for sex and consequently, there are either two kinds of sperms or two kinds of eggs. That has been the explanation which has gained almost universal acceptance. And the proof? Cytological evidence of gamete dimorphism and experimental evidence of the more or less one to one ratio of males and females. It seems like a logical and unassailable explanation.

Mercurialis annua is unique among experimental plants inasmuch as it can be used to test out the validity of the assumption that one or the other of the sexes is heterozygous for sex. Isolated male plants produce seeds and such seed when germinated gives rise to male plants only. The importance of that phenomenon cannot be overemphasized since the male plant without the intervention of the female plant registers its genetic constitution. How does it do it? It produces its own embryo sac with an egg apparatus. It produces pollen grains. Pollination takes place followed by fertilization and embryo formation. If males are heterozygous then two kinds of pollen grains should be produced and therefore two kinds of offspring male and female. But all the offspring of all the males that produce seed are male (Yampolsky, 1919).

Isolated female plants produce seed and such seed when germinated give rise to female plants only. The female plant without the intervention of the male plant registers its genetic constitution. How does it do it? It produces its own pollen grains with their generative cells. Pollination takes place followed by fertilization and embryo formation. If females are hetero-

zygous then two kinds of offspring should be produced, male and female. But all the offspring of all the females that produce seed are females (Yampolsky, 1919).

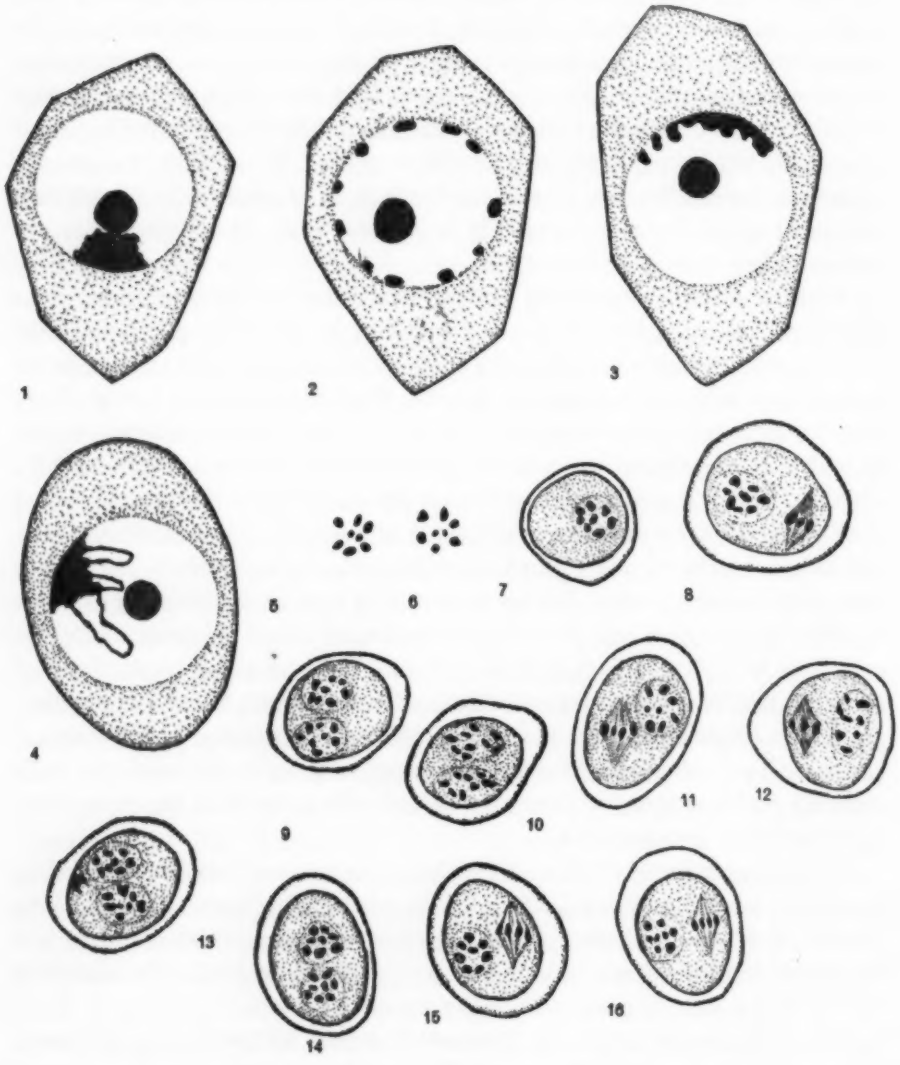
The pollination of female plants by male plants results in seed that produce male and female offspring. Cytologic and genetic evidence obtained from *Mercurialis annua* does not lend any support to the conception of gametic dimorphism. Are we to regard that plant as a non-conformist and therefore outside the pale of consideration? On the contrary, its possibilities should be exploited to the fullest extent. If selfed males and females can be obtained in *Rumex*, in *Lychnis*, in *Humulus*, in *Elodea* and the other plant forms for which it is claimed that sex-chromosomes are present, they should be tested out.

Until a direct relationship can be established between chromosomes and form and function we are not justified in ascribing particulate inheritance to the chromosomes. In spite of our advances in the study we cannot say with any degree of finality that chromosomes bring about definite morphological expressions. Why is it not just as tenable to say that chromosome form and number constancy are expressions of the cell's activity. The cytogeneticist forgets that between the initiation of the steps that result in a two-celled embryo and all the countless divisions that result in a highly complex plant other forces have intervened. He forgets that differentiation may also be a matter of spatial distribution of cells. A dividing cambium cell does not predetermine which of its two daughter cells is to be xylem, which is to be phloem. Position alone appears to determine that. In the mature individual cell adjustment, tissue adjustment, and organ adjustment, take place. Cells and organs undergo environmental changes. Two cells isolated are environmentally different from two cells exerting pressure upon one another. Many cells in contact are in an even more modified environment.

To look at a gamete cell with its chromosome complement—a cell that has been fixed and stained, all of whose parts have been congealed into inaction and to read therefrom the profound processes of development is a too great simplification of a yet only partly solved problem. We persist in saying that a part is greater than the whole.

The polygamous plants of *Mercurialis annua* bridge the gap between males and females. These intersexual forms show a graded series between males and females. I have pointed out (Yampolsky, 1930) that intersexualism expresses itself in any part of the plant and in varying degrees. Aside from the appearance simultaneously of male, female, and hermaphrodite flowers, polygamous forms may also produce modified male inflorescences. This study concerns itself with the cytology of male flowers on poly-

gamous forms. Lest there be any doubt as to the nature of the sex of the plants examined it must be emphasized that all polygamous forms start out as females and produce female flowers exclusively over a period of



Figs. 1–16. See text for explanation.

months. In the forms under observation not a single male or hermaphrodite flower was produced from May until July. After that sporadic male and hermaphrodite flowers appeared and as the plants grew in vegetative vigor, the increase in the numbers of males and hermaphrodites was ac-

celerated. Male branches and individual male flowers were fixed in Flemmings medium solution and stained with safranin and gentian-violet and orange G. At the same time male branches from male plants were also fixed and stained. For comparative material the prepared slides used for the study of male flowers (Yampolsky, 1925) were also examined.

All the conventional maturation stages that were observed in purely male material were found in the male flowers taken from the polygamous forms. During synapsis the pollen mother cells with their polygonal outlines show a very densely staining cytoplasm. The nuclear material is aggregated to one side—nucleolus and chromatin material are in a close snarl. The red stain of the nucleolus differentiates it from the massed chromatin. The pollen mother cell nuclei with the material heaped up on the periphery of the nuclear membrane, showed a definite orientation and raised the question whether that stage has its counterpart in the uninjured living cell. We forget that living matter fixed, is no longer living matter. Congealed water forms definite patterns from which we can deduce certain physical principles which do not necessarily hold for water in the liquid state. Protoplasm, a labile substance, subjected to the congealing properties of the fixing fluid, gives us a picture of dead irreversible protoplasm. Text figure 1 illustrates the degree of chromatic aggregation in the pollen mother cells. The massed material originates from the pro-chromosomes which in *Mercurialis annua* are arranged on the periphery of the nuclear membrane (fig. 2). In figure 3 several of the pro-chromosomes can be distinguished while others have passed into an amorphous state.

When the pollen mother cells have separated from one another and have rounded up, the chromatic material is no longer clumped but appears in the form of loops or threads. *Mercurialis annua* yields no good evidence either for parasynapsis or telosynapsis. As a matter of fact the significance of those stages, if they have any significance, is obscure. The conspicuous change is in the rounding up of the cell as a whole (fig. 4). Whatever physiological processes go on in the anther they bring about a separation of cells.

The preparations for reduction division in an already delimited sporophyll indicate a sexual segregation, physiological and morphological, long before the actual reductive stages. The steps leading towards the final division of the spore mother cell must be conceived as the fundamental ones in the long chain of sex expression that results in the production of gametes. If we could penetrate into the meaning of sexuality we could better understand the phenomenon known as meiosis. The newest meaning of sex, fresh from the pen of Darlington (1932) is nothing more than an amplification of Darwin's idea that hybridization increases variability. Darlington

is firmly convinced that pairing of chromosomes, maternal and paternal, occurs at meiosis and subsequent splitting results in a four strand chiasma. Under such conditions interchange of chromosomal segments can take place and does take place. Sexuality has no virtue save that it offers an opportunity for gene interchange, a crossing over, that results in variability. Meiosis has a justification; it encourages hybridity. Darlington, in common with many others, assumes that interchange of chromatic material takes place in the nucleus at meiosis only. The direct evidence for chiasmata, in spite of Jannsen's newest work (1924), is not convincing. Yet its theoretic value for genetic interpretations has been used with unusual effect in explaining genetic phenomena. If we admit the compact knot in synapsis then we must admit that whatever individuality chromosomes have had before entering a fusion stage, must have been lost in that stage. So intimate a mingling of nuclear material, must from the nature of the physical state of protoplasm, result in an exchange of material, not that exchange would necessarily mean a realignment of genetic entities. It seems inadmissible to infer that chromosomes resolved into chromatin and linin in intimate juxtaposition in the so-called resting stage could separate wholly uncontaminated. The debate between Sax (1932) and Darlington (1931) on chiasmata, in view of our inadequate knowledge of that phenomenon becomes an academic question of what would happen if one set of premises were correct and the other wrong.

The nucleolus during the meiotic stages becomes very conspicuous and even though it does not go through the complicated steps in division, its increase in size is an evidence that it is associated with active physiological processes. What these processes are I am not prepared to say. Because the nucleolus does not divide equationally is no indication that it is not concerned in the transmission of genetic properties. The extra nuclear nucleoles scattered through the cytoplasm during heterotypic division become an important part of the picture, even though we may have failed to find a particular function for the fragments. We have been so greatly impressed by what appears as an equational division of the chromatic material, that the rest of the cell becomes subordinate in our minds. No matter how thoroughly we trace back the units of heredity, and we have become satisfied that they have no accomplices, we can never get them to act alone. The chromosomes of the egg nucleus are in the cytoplasm of the embryo-sac from which they cannot escape. The sperm nuclei in the pollen tube are surrounded by the cytoplasm of the pollen grain. When they are discharged into the embryo-sac the cytoplasm is discharged with them. In hereditary transmission in the flowering plants, two cell complexes are concerned and whatever cytoplasmic properties the gamete cells have in

common with the adult from which they originate, they must be conceived as hereditary transmissions in as true a sense as are the 'Anlagen' which are presumed to reside in the chromosomes. A plastid from an egg of *Fucus*, an integral part of the female gamete, must be considered as evidence for the passing on of hereditary characteristics through the agency of the cytoplasm. Until we can definitely prove that the nucleolus which in *Mercurialis* exhibits marked increase in size during the maturation division in both the macro and microsporogenesis and beyond is useless, we must accept it as an integral part of genetic continuity. The specificity of protoplasm is, as we know, not limited to the nucleus. The study of blood relationships in animal forms must act as a reminder to us that other parts of the cell are concerned in determining whether the germ nuclei may be allowed to pair. Compatibilities and incompatibilities among flowering plants indicate to us that barriers may be let down or set up depending upon the specificities of the cytoplasm.

In discussing the heterotypic division in the male plant of *Mercurialis annua* (Yampolsky, 1925) I stated that differences in chromosome shape and form occur but no chromosome behaves in a manner which would point it out as different from any other. I have never understood the reasoning as to why a sex chromosome should behave differently from any other chromosome during division. Nor am I able to understand why a chromosome that lags behind during the division stages is necessarily identified with sex tendencies. Unpaired chromosomes in crosses involving the mating of two forms differing in chromosome number show such aberrant behavior and certainly no one would consider this behavior as having anything to do with sex. In *Mercurialis annua* the chromosomal variations do not warrant the assumption that chromosomal differences of distinct male and female quality are present. It is in the homeotypic division, that the variations in chromosome size and form appear most pronounced. Just as in the male, so too in the polygamous form, the homeotypic chromosomes in many of the polar views show two smaller chromosomes surrounded by six larger ones (figs. 5 and 6). That this is but a chance arrangement becomes evident from the study of a large number of polar views. The position of the chromosomes in relation to one another can have no significance since they are but transitory stages in a long process which results in the formation of the pollen grains. At this stage too the first outlines of what is to be the region of the nuclear membrane can be seen because of the difference between the density of the cytoplasm around the chromosomes and the rest of the cytoplasm.

The condition of pairing of chromosomes is most commonly met with in the diploid organism and particularly during the maturation phenomena.

In the haploid condition in *Mercurialis annua* pairing occurs, usually between chromosomes of equal size. Figures 7, 8, 9, 10 male and polygamous plants, show such pairing. The observations are of interest because they do not involve any of the theoretical requirements as to pairing. The chromosomes do not maintain constancy in size nor in form. Without actually measuring the chromosomes it can be seen that the total mass represented by a group of eight chromosomes may be equal to, may be less, may be greater than, that of a neighboring set of eight chromosomes. The chromosomes may be ovoid, spherical, or irregularly polygonal in outline, their edges may be rough or smooth. Figures 7 to 16 taken from male and polygamous plants show similarity in the life history of the two gametes. What has already been said for the nuclear figures of the male plant (Yampolsky, 1925) can be said for the nuclear figures in the male flowers on the polygamous plants.

The quest for sex chromosomes has led to their discovery in unexpected places. The breeding experiments of Shull (1914) between the phenotypic hermaphrodite *Lychnis* and the dioecious female lead him to conclude that some of the hermaphrodites were really genetic males. Shull's hypothesis finds a beautiful substantiation in Belar's (1927) cytological investigation of that form. Genetically and cytologically the hermaphrodite is not an hermaphrodite; it is a male with conspicuous x and y chromosomes present in both the male and female elements of the flowers.

Miss Pastrana (1932) reports an unusual mode of sex determination in *Begonia Schmidtiana*. The sporophyte chromosome number in that form is thirteen—six paired chromosomes and one unpaired chromosome. The unpaired chromosome has to do with sex determination. The female flower of the monoecious plant has thirteen chromosomes; the male flower has twelve chromosomes. The unpaired chromosome fails to enter the stem initial from which the male flower develops. Consequently only one kind of pollen grain is produced—one with six chromosomes. In the reduction division that goes to form the megaspore, the unpaired chromosome goes undivided to one pole and the embryo sac arises from a nucleus with seven chromosomes.

In *Lychnis* form and function do not necessarily agree. A phenotypic hermaphrodite with its hermaphrodite flowers having stamen and pistil, is a genotypic male. What is the significance of the external expression of that plant? Of no significance! Where does maleness reside? In the gametes! The gametes alone express the sex of the plant since the phenotypic expression does not parallel the genotypic constitution of the plant. Male and female elements in the hermaphrodite flower mean nothing. The plants are only apparent hermaphrodites in reality they are males. One

may very well ask the question: "What determines the hermaphrodite expression?"

I must recall Correns' (1907) and Bateson's (1909) classic examples of crosses between *Bryonia dioica* and the monoecious *Bryonia alba* which resulted in the production of male and female sterile hybrids, recognized by their external appearance, an instance where morphology not physiology is used for sex identification. From these results Correns concluded that male *Bryonia dioica* was heterozygous for sex and Bateson from the same results concluded that the female *Bryonia dioica* was heterozygous for sex. What is the significance of the outward expression of sex? Of great significance! Where do maleness and femaleness reside? In male and female expressions in the sporophyte. What about the gamete? There are no gametes, the plants are sterile. Male and female elements are expressed by sterile male and female flowers. If those plants could be made to express themselves the male would be heterozygous—Correns; homozygous—Bateson; the female would be homozygous—Correns; heterozygous—Bateson. In appearance they are males and females; in reality they are non-entities, not even neuters.

Miss Pastrana's observations raise a number of questions. She herself says that the loss of a chromosome immediately presupposes a somatic reduction division which is later followed by a true reduction division. The germination of the macrospore with seven chromosomes to form the embryo-sac implies a selective mortality. What forces determine which cells are to be sacrificed? Such an assumption embodies a sex determining force independent of the one that regulates the differentiation of embryo sac mother cell tissue from pollen mother cell tissue. The contentions of Miss Pastrana would have been strengthened if she had succeeded in showing the fate of the chromosome that failed to enter the stem initial from which the male flower developed. In connection with these observations I wish to call attention to Sandt's (1921) work on *Begonia tuberhybrida*. He found pistillody present. An anther sac filled with pollen grains shows at its apex an embryo sac. If a male flower becomes so because of the loss of a chromosome how can it produce a structure with one chromosome more than it possesses?

In *Begonia Schmidtiana* somatic reduction occurs and is later followed by the so-called true reduction division. This new evidence is entered in the ledger, on the credit side of sex chromosomes. Nevertheless a curious paradox does exist. In dioecious flowering plants sex is determined at fertilization; in dioecious flowering plants, x and x or x and y determine sex; in dioecious liverworts it is x or y that determines sex. In the monoecious *Begonia* female sex is determined when x and y unite; the male sex is de-

termined at the end of a cycle when the sporophyte loses a chromosome. In the monoecious (hermaphrodite) *Marchantia* femaleness is determined at reduction division in the formation of the spore and maleness is determined during the production of male sex organs when a chromosome is lost. How can we reconcile these divergent claims? As long as we shall ascribe to chromosomes the importance in heredity that we do, we shall see in chromosomal behavior all that we expect to see.

It is my opinion that in our desire to explore the world for new discoveries we often take painted scenery along so that when we come to barren wastes we can have the similitude of tropical scenery. We carry our categories with us. Sex falls into certain categories. Categories are man made. To classify, to label, to place into definite compartments biologic units that apparently belong together, is decidedly a human trait. The terms male and female connote circumscribed biologic units, units that have very close resemblances as well as very striking differences. Impressed by the differences we fail to detect the very fine gradations that exist, gradations which may insensibly bridge the differences that are conspicuous to the eye. Nineteen years of observation on *Mercurialis annua* have convinced me that obligate males and obligate females are but the extremes of a variable series. The *n*-numbers of sex forms refuse to submit themselves to the concept that sex is an alternative kind of inheritance. Neither sex categories nor sex chromosomes hem in the variability of sex expression exhibited by *Mercurialis annua*.

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Spathuliformae, a new section of Codonanthe

LYMAN B. SMITH

(WITH FIGURES 1–6)

In the process of studying some of Professor I. W. Bailey's collections from British Guiana, I came upon a peculiar specimen of *Gesneriaceae* which he had tentatively labelled as *Codonanthe*. The anthers had the irregular dehiscence and broad connective (fig. 3) which distinguish *Codonanthe* from the remainder of the family, but the filaments were fused into a broad ribbon attached to the ventral portion of the corolla-tube and the calyx consisted of but two lobes of very unequal size. Since all known species of *Codonanthe* had five-parted calyces and were supposed to have free filaments,[1] I at first supposed that Professor Bailey's material constituted a new genus.

However, a careful dissection of material of *Codonanthe cornuta*, *C. Hookerii* and *C. gracilis* soon demonstrated that, contrary to expectation, the filaments were fused although quite inconspicuously in the case of *C. Hookerii*. Also I noted that *C. cornuta* closely resembled the material in question in all but the form of the calyx, which was intermediate between the two-lobed type and the equally five-lobed type of *C. gracilis*, the type species of the genus. In *C. cornuta* the calyx is deeply cleft on each side of the dorsal lobe and much less between the four ventral lobes. This is evidently what Miquel referred to when he described the calyx as "spathaceo-fissus."[2] The failure of the filament character and the transition shown between the five-lobed and two-lobed calyces demonstrate that Professor Bailey's material belongs in the genus *Codonanthe*, but at the same time it is obvious that the genus is composed of two distinct sections as follows:

Eucodonanthe, calyce aequaliter 5-partito: corollae tubo amplo, basi postice gibbo: filamentis basi in vaginam brevem connatis. *C. gracilis*, species typica.

Spathuliformae, sect. nov., calyce distincte inaequaliterque bipartito, parte ventrali majori, spathuliformi, plus minusve 4-partita vel integra: corollae tubo gracili, basi postice calcarato: filamentis basi in vaginam elongatam connatis. *C. calcarata*, species typica.

Professor Bailey's material is then a new species of the section *Spathuliformae* and may be characterized as follows:

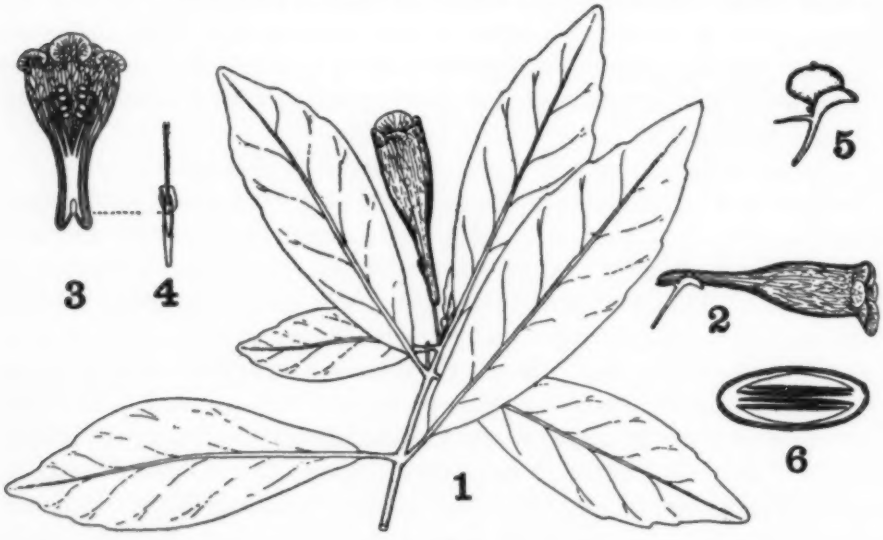
Codonanthe bipartita, spec. nov., caule elongato, ramoso, glabro: foliis oppositis, subtenuibus, glabris, ad 8 cm. longis, late oblanceolatis, integris vel

[1] Fritsch in Engl. & Prantl, Nat. Pflanzenf. **4:** Abt. 3 b: 171. 1894.

[2] *Nematanthus calcaratus* Miquel in Linnaea, **22:** 473. 1849.

ad apicem versus grosse sinuoso-dentatis, 5 mm. petiolatis: floribus axillaribus, graciliter pedicellatis; calyce inaequaliter bipartito, parte dorsali anguste lanceolata, parte ventrali integra, oblonga, obtusa; corolla alba, sicca aurea, 25–30 mm. longa, basi anguste tubulosa et calcarata, tum ampliata, infundibuliformi-campanulata, limbo patenti, 5-lobo; staminum filamentis basi in vaginam elongatam connatis: fructu baccato, valde lateraliter compresso. Figures 1–6.

BRITISH GUIANA: Kartabo region, 1920, *I. W. Bailey 181* (type); same, *I. W. Bailey 110*. The following numbers appear to be conspecific: Waini River, Northwest District, lat. 8° 20′ N., long. 59° 40′ W., 1923,



Figs. 1–6.

CODONANTHE BIPARTITA L. B. Smith

1. Branch ×1. 2. Lateral view of flower ×1. 3. Corolla cut dorsally and laid open ×1. 4. Calyx and pistil, showing dorsal gland, ×1. 5. Calyx and fruit ×2. 6. Enlarged diagrammatic cross-section of fruit.

De La Cruz 3735; upper Mazaruni River, long. about 60° 10′ W., 1922, *De La Cruz 2294.*

Codonanthe bipartita is quite easily recognizable even in fruiting condition on account of its peculiar calyx. In addition the elongate seeds all lie parallel, as indicated in figure 6, and thus cause the soft fruit to assume a strong lateral compression.

GRAY HERBARIUM OF HARVARD UNIVERSITY

INDEX TO AMERICAN BOTANICAL LITERATURE

1931–1933

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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